4.—ANATOMY OF THE QUOKKA
[*Setonix brachyurus* (Quoy and Gaimard)]

PART I.—EXTERNAL MORPHOLOGY AND LARGE INTESTINE.

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Read: 10th June, 1947.

INTRODUCTION.

A.—General.

The quokka (*Setonix brachyurus*) is a diprotodont marsupial of the family *Macropodidae.* Its body is about as big as that of a large cat, but the whole animal is rather squat and has not the graceful appearance of the larger members of the family. In certain attitudes it looks very like an enormous rat, particularly when it is feeding on some loose object such an apple, when the food, resting on the ground is held between the forelimbs, the whole body being outstretched and close to the ground (pl. 1).

The animal is now almost confined to Rottnest Island which is 11½ miles west of Fremantle, but, according to Shortridge (1909 p. 813) it once was "Very plentiful among coastal thickets and swamps of the South-West, not extending inland" and it also occurred "sparingly as far north as Moore River." He further noted that it is not found on Garden Island but recorded it from ". . . Bald Island to the east of King George's Sound, and on Twin Peak and probably other islands off Esperance." Troughton (1941, p. 196) and Glauert (1934, p. 32) give similar accounts of its distribution.

Dutch navigators of the 17th century who landed, more by chance than intention, in a few places on the west coast of Australia or on outlying islands, noticed animals which were probably or certainly quokkas. The first published record is, according to Troughton (1941, p. 197), by Samuel Vlockersen, who, in 1658, mentioned a ". . . wild cat resembling a civet cat, but with brown hair."

On December 30, 1696, van Vlaming and his men landed on a large island. "On exploring it they were struck with the large number of rats' (wallabies') nests to be seen and gave it the name of 'Rottnest Island.' " (Battye, 1924, p. 40).

One of Vlaming's party wrote regarding Rottnest Island, "There are very few birds there and no animals, except a kind of rat as big as a common cat, whose dung is found in abundance all over the island." (Major, 1859, p. 121).

The quokka was identified by the French naturalist Bailly and others in 1801 as a "small species of Kangaroo" (Glauert, 1929, p. 38) but was first systematically described by Quoy and Gaimard (1830, pp. 114-116). The specimen, which had been found dead at King George Sound, was named *Kangarus brachyurus.* Wood Jones (1924a, p. 261) indicates that the generic name *Setonix* was given to it by Lesson, 1842.

B.—POSITION OF SETONIX IN THE FAMILY MACROPODIDAE.

The quokka differs from most other macropods in dentition, having large sectorial pre-molars and small, low-crowned molars. This was recognised, figured, and recorded, together with some external measurements and the character of the skull, by Thomas (1888, p. 60).

Bensley (1903) has discussed at length the phylogenetic relationships of the marsupials. In the case of *Setonix,* he recognises the resemblance between its pre-molars and molars, and those of the Tree Kangaroo (*Dendrolagus*) and of *Dorcopsis.* However, he suggests that, through the loss of the canines and the purely terrestrial character of the foot, it is probably a member of the group of Small Wallabies of genus *Macropus*; it has paralleled *Dendrolagus* in its feeding habits. (1903, pp. 151-152 and p. 202.)

Troughton (1941, p. 196) recognises the peculiarity of the dentition of the quokka and its resemblance to that of the Tree Kangaroo (*Dendrolagus*) and of the Dorcopsis Wallabies, but he places it with *Thylogale* under the general heading "Scrub or Pademelon Wallabies."

Wood Jones (1924a, pp. 220 and 261) places the animal in the brachydont section of the sub-family *Macropodinae;* this section includes *Dendrolagus* and *Dorcopsis,* which *Setonix* resembles in the nature of its pre-molar and molar teeth, but from which it differs in having no canine teeth and in having a very short tail, scarcely twice the length of the head—whence, of course, its specific name "brachyurus."

Lydekker (1894, pp. 41-42) and Le Souef and Burrel (1926, pp. 175-176 and 200), apparently not realising the significance of the quokka's dentition, place it in the genus *Macropus* and seemingly in the sub-genus *Thylogale,* which would be correct if one relied solely on externals and neglected the dentition.

According to Wood Jones (1923, 1924a) the quokka's position in the animal kingdom is:—

- Class Mammalia.
  - Sub-Class Didelphia.
    - Order Marsupialia.
      - Sub-Order Sydnactyla.
        - Section Syndactyla Diprotodontia.
          - Family Macropodidae.
            - Sub-Family Macropodinae, brachydont section.
              - Genus *Setonix.*
                - Species *brachyurus.*

C.—PURPOSES AND METHOD OF THIS STUDY.

Apart from the observations of Bensley and Thomas there is no published information on the general characteristics and habits of *Setonix,* except Fleay's article (1936, pp. 153-155) dealing with its birth habits, nor has anything been written about the anatomy of its soft parts. Beddard (1908 p. 568) does indeed give measurements of the intestine, but does not describe it.

This paper is intended to be the first part of a fairly detailed discussion of all anatomical systems of *Setonix,* which should be the basis for comparison with local macropods and with other members, *Dendrolagus* and *Dorcopsis,* of the brachydont section of the sub-family Macropodinae. Such comparisons may throw further light on the relationships of *Setonix.*

A single adult male specimen of the Garden Island Wallaby [*Macropus* (*Thylogale*) *eugenii derbianus* (*Gray*)], which will be called *Macropus eugenii* throughout this paper, became available towards the end of the investigation. References have been made to *M. eugenii* in the text and a section has been included dealing briefly with the pattern of its hindgut, comparing it with that of *Setonix.*

Until it is possible for full comparisons to be made between *Setonix* and other macropods, it seems well to report in detail on the external features and hindgut of the seven specimens available so that full information would be provided for future comparisons. The examination of a number of specimens should, to some extent, preclude the drawing of false conclusions regarding the typical anatomy of *Setonix,* due to individual peculiarities and variations.

Two dead pouch embryos, one 70 millimetres and the other 110 millimetres from tip of snout to base of tail, were recovered from specimens in my possession. Notes on the ileo-coecal and colic regions of these embryos have been made enabling comparisons to be drawn between them and adults. Further details of the 110 millimetre specimen are given on p. 143 under IV ("Notes on the Natural History of the Quokka").

Some observations of natural history have been made on the living animals and these, together with a problem regarding the insular distribution of the Garden Island Wallaby and the Quokka, are included as Section IV at the end of the paper.

Many of the figures included in this paper were prepared by placing the specimen about 9 inches below a 3′ x 2′ frame, subdivided by cords to give a 25 mm. square mesh. The particular structure was drawn on to graph paper ruled into 5 mm. squares.

This investigation, part of the course for an Honours B.Sc. degree in the University of Western Australia, was carried out under the supervision of Professor G. E. Nicholls, while I was the recipient of a Hackett Research Scholarship.

In addition, my thanks are due to Mr. L. Glauert, Curator of the Perth Museum, to Mr. K. Sheard, of C.S.I.R. Division of Fisheries, and to Mr. E. P. Hodgkin, Lecturer in Zoology at the University of Western Australia, for kind help and advice in the preparation of this paper. I also wish to thank the Rottnest Board of Control for permission to obtain specimens, and Mr. N. Love, of Rottnest, who very kindly obtained and forwarded to me three male and three female specimens which were all adult or approaching adulthood (see p. 63), thus adding to my own collection of one small immature male. Some of the specimens were kept alive and in good health in a large cage at the Department of Biology of the University of Western Australia.

II.—EXTERNALS.

A.—Introduction.

Description of externals in a normal animal may be an important pre-requisite to physiological research on the animal. This is made apparent by the recent work of Bolliger (1938, 1943 a and b, 1946) on the changes in integumental structures of *Trichosurus vulpecula*, resulting from the administration of sex hormones and gonadotropin. If similar work is ever carried out on *Setonix*, familiarity with the externals in their normal, healthy state would be invaluable in detecting any change in them after treatment of the animal with the above compounds. Particularly important, in this respect, would be a knowledge of the colour, length and concentration of hair, and of any pigmentation of the skins, in the region of the pouch, scrotum and cloacal orifice.

The general form and appearance of the quokka have been described already (p. 59). (See also pl. 1.) Apart from differences in actual, and in some cases, of relative size, the external morphology of *Setonix* does not appear to differ in any important particular from that of other macropods.

Much of what I describe of the externals, particularly the pelage, has been recorded by Quoy and Gaimard (1830, p. 114), Waterhouse (1846, p. 162), Thomas (1888, pp. 60-61), but the inclusion of figures, not given in earlier descriptions and illustrating certain external features, will perhaps justify some repetition.

The tables of measurement and ratios emphasise features some of which have been recognised in past descriptions of single specimens.

The condition of the premolars has been taken as the criterion of adulthood in this investigation. At least one animal (specimen 3, female) in my collection was sexually mature, as indicated by the presence of an embryo in the pouch, but I consider that, judged by its dentition, it was not strictly adult. Though sexual maturity may be just as legitimate a base from which to measure ages, it is not as practical as the condition of the teeth.

From an examination of my specimens and of skulls of *Setonix* in the collections of the Department of Biology in the University of Western Australia, it seems that there is in the right and left upper and lower jaws of the young animals, a *milk* sectorial premolar. This is 4 mm. long and has two shallow vertical grooves about 0.5 mm. apart and placed at about the middle of the length of the tooth, running from its cutting edge towards the gum. In the adult this tooth is replaced by a larger *permanent* sectorial premolar, 6 mm. long and with three shallow grooves.

Thus, by examination of the sectorial premolar of *Setonix* its *dental* age can be determined. In this respect those with the shorter, milk sectorial premolars are regarded as immature, those with the longer permanent sectorial premolars as mature.

Specimens 2, 5, 6, and 8 were mature, 1, 3, and 4 were immature in their premolar dentition.

Specimen 1 (a small male) was not included in measurements.

In describing the externals of *S. brachyurus* I have largely followed Finlayson (1930, pp. 47-56, 1932, pp. 148-67), and Wood Jones (1920, pp. 360-73; 1922, pp. 119-30; 1923; 1924a; 1924b, pp. 145-8).

B.—METHODS OF MEASUREMENT USED IN THIS PAPER.

All measurements have been made to the nearest millimetre.

1. *Total Body Length.*

The specimen was straightened out without unnatural stretching, and the length taken with a cord from the tip of the snout to the base of the tail, following the curves of the mid-dorsal line (Finlayson, 1930, p. 55; Wood Jones, 1923, p. 12). By flexing the tail at right angles to the body, its base was better defined.

2. *Measurements on Head.*

All measurements were made with calipers. Measurements a. to e. were used by Finlayson (1932, p. 165, Table 1). In addition the recording of the maximum transverse width of the head and the width of the head at the base of the ears, is suggested by Thomas' statement (1888, p. 61) that the skull of *Setonix* is strongly built and broad in proportion to its length.

a. Rhinarium to eye.
From tip of rhinarium to anterior canthus of eye.

b. Eye.
Canthus to canthus.

c. Eye to ear.
From posterior canthus of eye to notch between tragus and antitragus of ear.

d. Length of ear.
From notch between tragus and antitragus to tip of ear (see also Wood Jones, 1923, p. 13, fig. 10).

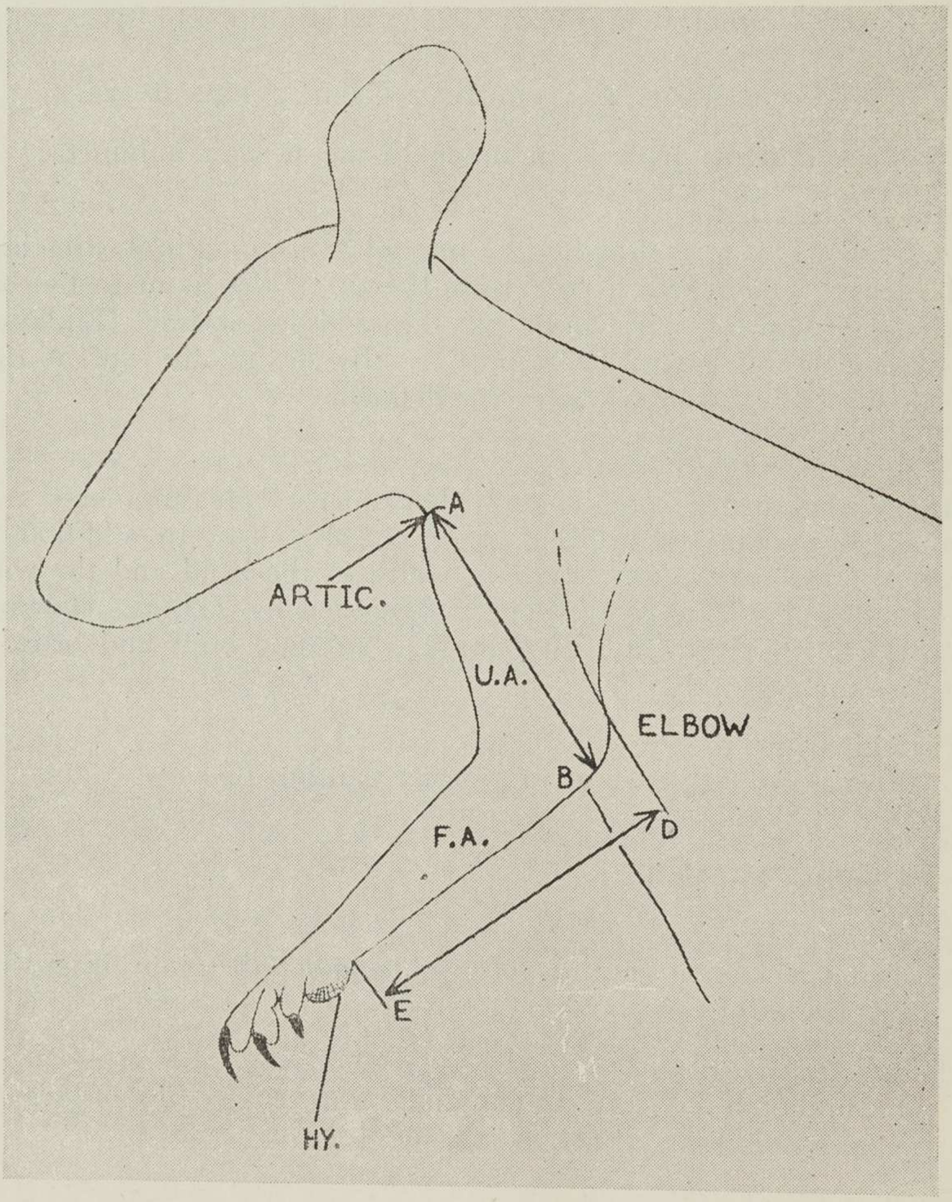
e. Breadth of ear.
Maximum breadth, without distortion, of external ear from its cephalic to its caudal margin.

f. Maximum transverse width of head.
Corresponds roughly to articulation of lower jaw with upper.

g. Transverse width of head at base of ears.
Between inflated areas of the cartilaginous portion of external auditory meatus near base of ear.

3. *Measurements on Forelimb.*

All these were made with calipers. Finlayson (1930, p. 55, Table 1) lists the length of the "humerus" and "ulna radial length." These appear in a table with flesh measurements and so presumably were made in the flesh, despite the use of skeletal names. In the same table c. and f. of the measurements detailed below are given. The statement by Waterhouse (1846, p. 162) that the forefeet of *Setonix* are proportionately rather large suggests the additional measurements of the breadth of the hand and length of the third finger.



Text fig. 1.—**S. brachyurus.** Lateral semi-diagrammatic view of head and shoulders to show length A-B of upper arm and D-E of fore arm.

ARTIC.—region of articulation of humerus with scapula; F.A.—forearm; HY—hypothenar pad; U.A.—upper arm.

a. Length of upper arm.
Taken from articulation of humerus with scapula to the elbow. (text fig. 1). The articulation could be felt through skin and muscle.

b. Length of forearm.
Taken from elbow to proximal end of hypothenar pad on palm of manus (text fig. 1).

c. Length of hand.
Taken from proximal end of hypothenar pad to tip of third digit, excluding the nail.

d. Breadth of hand.
Taken from preaxial base of first finger to postaxial base of fifth finger.

e. Length of third finger.
Taken from line joining base of the cleft between 3rd and 2nd, and 3rd and 4th fingers to the tip of finger, excluding nail.

f. Length of claw of third finger.
From base to tip.

4. *Girth of Chest.*

This measurement was used by Finlayson (1930, p. 55, table 1; 1932, p. 165, table 1). It is the maximum girth of the thorax, taken with a cord, in the diaphragmatic region.

The measurement is not very satisfactory because there is no very definite external point from which it can be taken. I also tried taking the measurement at a point defined by reference to the ribs, but this did not seem any more satisfactory.

5. *Measurements on hind limb.*

All these were made with calipers. Finlayson (1930, p. 55, table 1) gives the lengths of "femur" and "tibia," and I have made the same assumption regarding them as I did for "humerus" and "ulna-radial" above; he also gives measurements for c, d, e, and for which I give results.

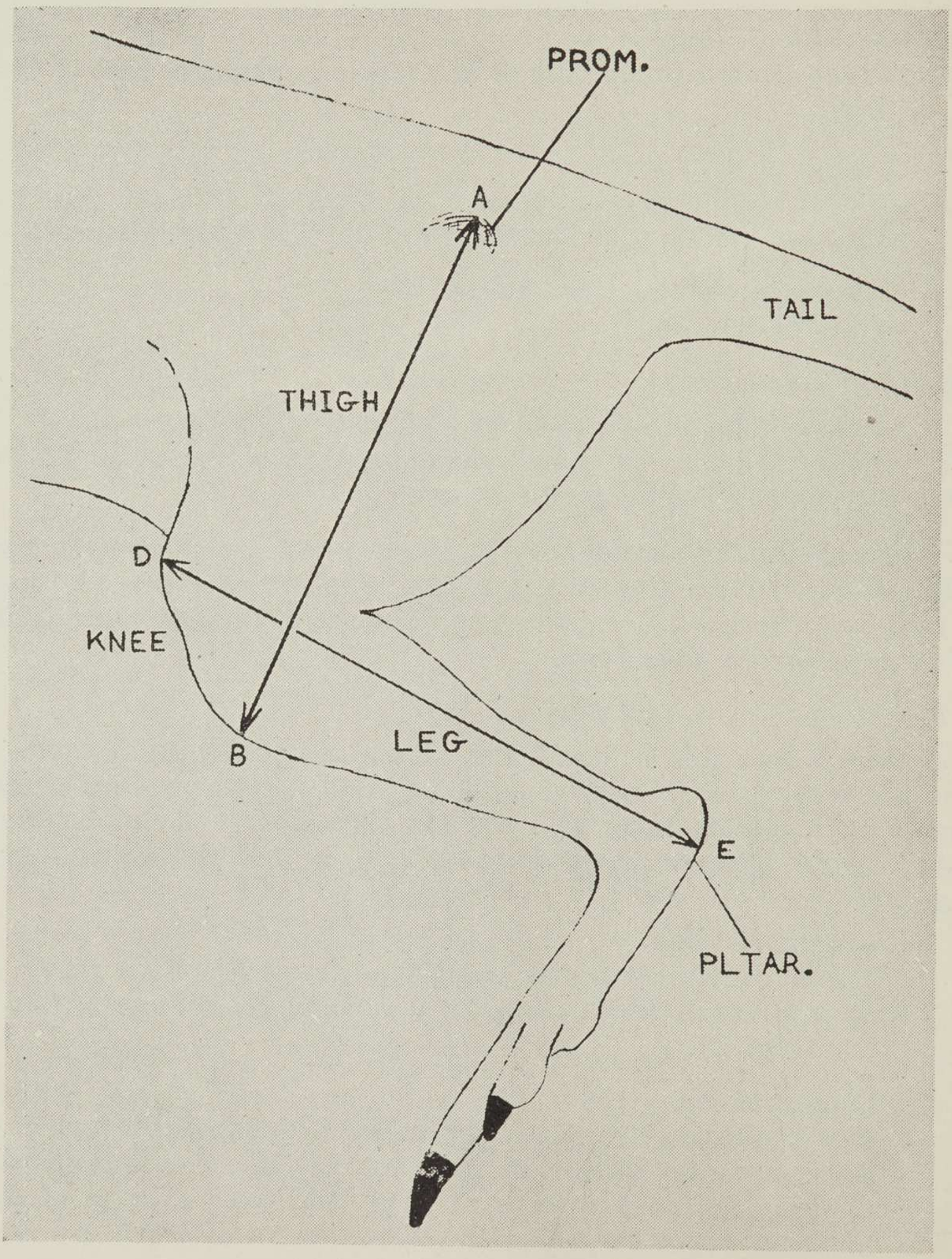
a. Length of thigh.
Taken with thigh flexed at right angles to leg, from region of acetabulum in which the great trochanter could be felt, to knee (text fig. 2).

b. Length of leg.
Taken with leg flexed at right angles to thigh and to foot, from knee to plantar surface of heel (text fig. 2). The measurement therefore includes portions of thigh and foot; in spite of this, the points between which the measurement is taken are more satisfactory than others which might give the true length of the leg.

c. Length of foot.
Taken from "the point of the heel to the tip of the most distant

toe, but the claw must not be included in the measurement." Wood Jones, 1923, p. 12 and fig. 9). The most distant toe in this case is the fourth.

d. Breadth of foot.
Bensley (1903, p. 175) takes this measurement in a pentadactyl animal such as *Perameles* across the foot immediately behind the hallux. There is no hallux in the quokka, so the measure-



Text fig. 2.—**S. brachyurus.** Lateral semi-diagrammatic view of hind-quarters to show length A-B of thigh and D-E of leg.

PLTAR.—Plantar surface of heel; PROM.—prominence (? great trochanter).

ment is taken across the foot from preaxial base of syndactylous toe to postaxial base of fifth toe.

e. Length of fourth toe.
Taken from base of cleft between the fourth and fifth toes to tip of fourth toe, excluding nail.

f. Length of claw of fourth toe.
Taken from its base where it joins the fourth toe to its tip.

6. *Measurements on tail.*

a. Length of tail.
As indicated in the tables of measurements and ratios, both Wood Jones's and Finlayson's have been employed (Wood Jones, 1923, p. 12, fig. 9; Finlayson, 1930, p. 55). Owing to the ill defined nature of base of tail even when tail is flexed at right angles to body, Wood Jones's does not seem as satisfactory as Finlayson's, which has for its proximal point the posterior margins of cloaca, which are better defined than base of tail.

b. Girth of tail.
Taken at its base which, as already stated, is not well defined, so that this measurement is rather unsatisfactory.

Specimen Number	6	5	4	7	3	2
Sex	♂	♂	♂	♀	♀	♀
Total Length	527	488	465	500	465	537
Rhinarium to Eye	40	40	38	34	34	38
Eye—Canthus to Canthus	13	13	13	11	11	15
Eye to Ear	43	43	42	40	40	45
Length of Ear	42	40	43	44	39	37
Breadth of Ear	30	30	32	30	28	27
Maximum Width of Head	53	52	53	51	51	54
Width of Head at Base of Ears	41	45	46	35	43	45
Length of Upper Arm	69	64	68	57	55	58
Length of Foream	83	80	83	75	70	73
Length of Hand	30	29	36	31	30	32
Breadth of Hand	16	15	20	15	15	15
Length of 3rd Finger	13	11	15	11	11	12
Length of Claw of 3rd Finger ..	9	9	9	10	7	9
Girth of Chest	272	272	317	263	263	270
Length of Thigh	121	115	116	112	102	111
Length of Leg	145	144	127	143	128	135
Length of Foot	108	110	112	102	101	105
Breadth of Foot	17	19	21	19	16	18
Length of 4th Toe	34	33	36	34	32	34
Length of Claw of 4th Toe	21	17	11	16	13	16
Length of Tail (Finlayson)	332	337	350	313	288	321
Length of Tail (Wood Jones) ..	294	320	321	292	258	302
Girth of Tail	102	113	106	110	84	90
Weight in lbs. (preserved specimens	5¼	5	6½	5¼	5	7

TABLE I.—Body Measurements (in millimetres) on **S. brachyurus.** Details of dental age of specimens, see p. 63.

Specimen No.	1
Sex	♂
Total Length	590
Rhinarium to Eye	57
Eye—Canthus to Canthus	15
Eye to Ear	47
Length of Ear	64
Breadth of Ear	35
Maximum Width of Head	55
Width of Head at Base of Ears	46
Length of Upper Arms	100
Length of Forearm	114
Length of Hand	45
Breadth of Hand	25
Length of 3rd Finger	17
Length of Claw of 3rd Finger	15
Girth of Chest	397
Length of Thigh	151
Length of Leg	233
Length of Foot	144
Breadth of Foot	23
Length of 4th Toe	45
Length of Claw of 4th Toe	25
Length of Tail (Finlayson)	509
Length of Tail (Wood Jones)	471
Girth of Tail	180
Weight in lbs. (preserved specimen)	13½

TABLE II.—Body measurements (in millimetres) on **M. eugenii.**

C.—EXAMINATION OF MEASUREMENTS.

Measurements were completed before I had thought of comparing the measurements of males and females of *Setonix* or of using this method of comparing *Setonix* with other macropods.

The following is an analysis of these measurements, but the results can only be regarded, at the best, as suggestions.

1. *Source of error in flesh measurements.*

Apart from the "personal equation" these are:—

a. State of preservation.
In this investigation all specimens had been preserved in museum fluid for various periods up to two months prior to measurement, and therefore soft tissues, in contrast to skeletal structures, may have been distorted, the amount of distortion differing in the various specimens.

b. Lack of definite landmarks.
The points between which measurements were taken were often not sharply defined, definition varying from specimen to specimen. This lack of definiteness is particularly apparent in measuring the length of body, made with reference to the ill-defined base of tail, in measuring the basal girth of tail and the length

of upper arm and thigh (head of humerus and great trochanter are sometimes difficult to find beneath the muscles).

c. "Give" of tissues.
A less important source of error than a. or b. is the yielding of tissues under the pressure of calipers.
Possibly the most satisfactory of all the flesh measurements, being least affected by the sources of error as set out above, is the length of the foot.

2. *Method of examination.*

In order to compare lengths in males and females of *S. brachyurus* and between them and the one specimen of *M. eugenii* measurements were converted into ratios by both—

a. dividing each measurement of a set for a given specimen, by the foot measurement of that specimen,

b. dividing each measurement of a set for a given specimen, by the total body length of that specimen.

It is considered that (a) is more satisfactory than (b)—Hersh (1941) and Lumer, Anderson & Hersh (1942) have indicated that it is desirable in such comparisons, to take as a base measurement which corresponds to the animal's total length at some fixed event within the animal's life history. It is thought that the length of the foot in the adult *Setonix* is reasonably related to the suspected body length at the time of its emergence from the pouch, that is, at the end of the "infant stage," a definite event in the growth cycle.

Adult body length is reached towards the end of the growth period and its use as a base may produce false ratios.

As stated earlier, it has been found that measurement of the length of the foot is also more satisfactory form the point of view of accuracy of measurement, than body length.

In testing for possible differences between either male and female of *Setonix* or between male and female *Setonix* and *M. eugenii* the following method was employed, which was considered adequate for such a small investigation as this involving a very few specimens; more involved statistical analysis with its conclusions, could well be very misleading. If the range of ratios for a given measurement on, say, male specimens of *S. brachyurus* does not overlap or fall within the range of ratios for the same measurement in females, then this is regarded as suggesting a difference, i.e. a sex difference, in the relative lengths of the particular structure measured, but no conclusions for or against a sex difference can be drawn if the range of ratios for that particular measurement for males overlaps or falls within that for females.

The same principle was observed in testing for possible differences between *S. brachyurus* and *M. eugenii.*

In some cases the difference between the range of ratios for a male and female specimen of *Setonix* is very small, in others it is large. By taking a bigger sample the range of ratios for one sex may overlap, or

There is a possible sex difference in:—

- i. Maximum width of head—that of female being the wider.
- ii. Length of upper arm—that of male being the greater.

The ranges of all other ratios for male and female either overlap or fall within each other and in such cases conclusions have not been made.

b. From Table V. (measurements for any one specimen divided by its body length).

The following are greater in male than in female:—

- i. Length of rhinarium to eye.
- ii. Length of upper arm.
- iii. Length of forearm.
- iv. Length of thigh.

The ranges of all other ratios for male and female either overlap or fall one within each other and in such cases conclusions have not been made.

4. *Suggested differences between* ***S. brachyurus*** *and* ***M. eugenii.*** (Measurements for any one specimen divided by its foot length.)

a. From Tables III and IV.
The following are greater in *M. eugenii* than in *S. brachyurus*:—

- i. Length from rhinarium to eye.
- ii. Length of ear.
- iii. Length of upper arm.
- iv. Length of forearm.
- v. Length of leg.
- vi. Length of tail (Finlayson and Wood Jones method).
- vii. Girth of tail.

The following are smaller in *M. eugenii* than in *S. brachyurus*—

- i. Total length.
- ii. Eye—canthus to canthus.
- iii. Eye to ear.
- iv. Breadth of ear.
- vii. Length of tail.
- v. Maximum width of head. There is a sex difference in this ratio in *Setonix*. The relative maximum width of head in *M. eugenii* is smaller than in either male or female *Setonix*.
- vi. Width of head at base of ears.

The ranges of all other ratios for *M. eugenii* fall within those for *Setonix* and in such cases no conclusions have been made.

	Combined Range ♂ & ♀	♂	♀
Total Length	4.15—5.11	4.15—4.88	4.60—5.11
Rhinarium to Eye	0.33—0.37	0.34—0.37	0.33—0.36
Eye—Canthus to Canthus	0.11—0.14	0.12	0.11—0.14
Eye to Ear	0.37—0.43	0.37—0.40	0.39—0.43
Length of Ear	0.35—0.43	0.36—0.39	0.35—0.43
Breadth of Ear	0.26—0.29	0.27—0.29	0.26—0.29
Maximum Width of Head	0.47—0.51	0.47—0.49	0.50—0.51
Width of Head at Base of Ears . . .	0.34—0.43	0.38—0.41	0.34—0.43
Length of Upper Arm	0.54—0.64	0.58—0.64	0.54—0.56
Length of Forearm	0.69—0.77	0.73—0.77	0.69—0.73
Length of Hand	0.26—0.32	0.26—0.32	0.29—0.30
Breadth of Hand	0.14—0.18	0.14—0.18	0.14—0.15
Length of 3rd Finger	0.10—0.13	0.10—0.13	0.11
Length of Claw of 3rd Finger	0.07—0.10	0.08	0.07—0.10
Girth of Chest	2.47—2.83	2.47—2.83	2.57—2.61
Length of Thigh	1.01—1.12	1.04—1.12	1.01—1.10
Length of Leg	1.13—1.40	1.13—1.34	1.27—1.40
Length of Foot	1.00	1.00	1.00
Breadth of Foot	0.16—0.19	0.16—0.19	0.16—0.19
Length of 4th Toe	0.30—0.33	0.30—0.32	0.32—0.33
Length of Claw of 4th Toe	0.10—0.19	0.10—0.19	0.13—0.16
Length of Tail (Finlayson)	2.85—3.12	3.06—3.12	2.85—3.07
Length of Tail (Wood Jones)	2.55—2.91	2.72—2.91	2.55—2.88
Girth of Tail	0.83—1.08	0.94—1.03	0.83—1.08

TABLE III.—Ratios—obtained by dividing each measurement made on a given specimen of **S. brachyurus** by a foot measurement of that specimen (see p. 69). The range only of such ratios for a given measurement on males or females is shown.

may diverge even further from, the corresponding set of ratios for the other sex. No allowance for this, nor any prediction as to which differences suggested here would be eliminated by examination of larger samples, has been made. This proviso applies also to examination for possible differences between *M. eugenii* and *S. brachyurus.*

In making comparisons, the ratios for male and female specimens were examined for any sex difference. Following this, comparisons between *S. brachyurus* and *M. eugenii* were made. If it had previously been found that, for any one measurement there may be a sex difference in the quokka, then comparisons were first made between the males of that animal and *M. eugenii* (male). Further, if the ratio for a given measurement in *M. eugenii* did not fall within the whole range for the same measurement in both male and female quokkas, then it was considered that a difference between both male and female quokkas and the male of *M. eugenii* was suggested.

Ratios in which there is no indication of a sex difference in *Setonix,* were compared as a whole with the same ratios for *M. eugenii.*

3. *Suggested difference between male and female.*

   a. From Table III. (measurements for any one specimen divided by its foot length).

Specimen No.	1
Sex	♂
Total Length	4.10
Rhinarium to Eye	0.40
Eye—Canthus to Canthus	0.10
Eye to Ear	0.33
Length of Ear	0.44
Breadth of Ear	0.24
Maximum Width of Head	0.38
Width of Head at Base of Ears	0.32
Length of Upper Arm	0.69
Length of Forearm	0.79
Length of Hand	0.31
Breadth of Hand	0.17
Length of 3rd Finger	0.12
Length of Claw of 3rd Finger	0.10
Girth of Chest	2.76
Length of Thigh	1.05
Length of Leg	1.62
Length of Foot	1.00
Breadth of Foot	0.16
Length of 4th Toe	0.31
Length of Claw of 4th Toe	0.17
Length of Tail (Finlayson)	3.53
Length of Tail (Wood Jones)	3.27
Girth of Tail	1.25

TABLE IV.—Ratios obtained by dividing each measurement made on **M. eugenii** by its foot measurement.

	Combined Range ♂ & ♀	♂	♀
Total Length	1.00	1.00	1.00
Rhinarium to Eye	0.07—0.08	0.08	0.07
Eye—Canthus to Canthus	0.02—0.03	0.02—0.03	0.02—0.03
Eye to Ear	0.08—0.09	0.08—0.09	0.08—0.09
Length of Ear	0.07—0.09	0.08—0.09	0.07—0.09
Breadth of Ear	0.05—0.07	0.06—0.07	0.05—0.06
Maximum Width of Head	0.10—0.11	0.10—0.11	0.10—0.11
Width of Head at Base of Ears	0.07—0.10	0.08—0.10	0.07—0.09
Length of Upper Arms	0.11—0.15	0.13—0.15	0.11—0.12
Length of Forearm	0.14—0.18	0.16—0.18	0.14—0.15
Length of Hand	0.06—0.08	0.06—0.08	0.06
Breadth of Hand	0.03—0.04	0.03—0.04	0.03
Length of 3rd Finger	0.02—0.03	0.02—0.03	0.02
Length of Claw of 3rd Finger	0.01—0.02	0.02	0.01—0.02
Girth of Chest	0.50—0.68	0.52—0.68	0.50—0.57
Length of Thigh	0.21—0.25	0.23—0.25	0.21—0.22
Length of Leg	0.25—0.29	0.27—0.29	0.25—0.29
Length of Foot	0.20—0.24	0.20—0.24	0.20—0.22
Breadth of Foot	0.03—0.04	0.03—0.04	0.03—0.04
Length of 4th Toe	0.06—0.08	0.06—0.08	0.06—0.07
Length of Claw of 4th Toe	0.02—0.04	0.02—0.04	0.03
Length of Tail (Finlayson)	0.60—0.75	0.63—0.75	0.60—0.63
Length of Tail (Wood Jones)	0.55—0.69	0.56—0.69	0.55—0.58
Girth of Tail	0.17—0.23	0.19—0.23	0.17—0.22

TABLE V.—Ratios obtained by dividing each measurement made on a given specimen of **S. brachyurus** by the total body length of that specimen (see p. 69). The range only of such ratios for a given measurment on males or females is shown.

b. From Tables V and VI (measurement for any one specimen divided by its body length).

The following are greater in *M. eugenii* than in *S. brachyurus*—

- i. Length from rhinarium to eye.
- ii. Length of ear.
- iii. Length of upper arm.
- iv. Length of forearm.
- v. Length of thigh .
- vii. Length of tail (Finlayson and Wood Jones method).
- viii. Girth of tail.

In i, iii, iv, and v there is a sex difference in *Setonix*, and, in each case, the corresponding ratio in *M. eugenii* is greater than that for either sex in *Setonix*.

There is only one measurement—maximum width of head—which is relatively smaller in *M. eugenii* than in *Setonix*.

The ranges of all other ratios for *M. eugenii* fall within those for *Setonix*, and in such cases no conclusions have been made.

5. *Conclusion.*

It has been emphasised that the sample of animals available for this investigation was small and consequently conclusions drawn from observations on differences in ratios between the sexes of *Setonix* and between *Setonix* and *M. eugenii*, merely suggest that further work on much larger samples of each genus may be of value in discovering definite differences between the two genera and between the sexes.

D.—EXTERNAL MORPHOLOGY AND HAIR.

General colour of dorsal surface of body, grey-brown; that of ventral surface a lighter silver-grey. Hairs of dorsal surface rather coarse, those of ventral surface finer.

1. *Head.*

a. Hair.

Hairs of head shortest towards tip of muzzle and longest towards ears. Largely of a rufous colour, reaching maximum intensity laterally in region of mystical and submental sets of vibrissae, and at bases of ears. On dorsal surface there is a smaller number of grey and dark brown or black hairs mixed with rufous ones. Ventral surface of lower jaw covered with light grey hairs.

b. Form (Pl. I and II; text fig. 3).

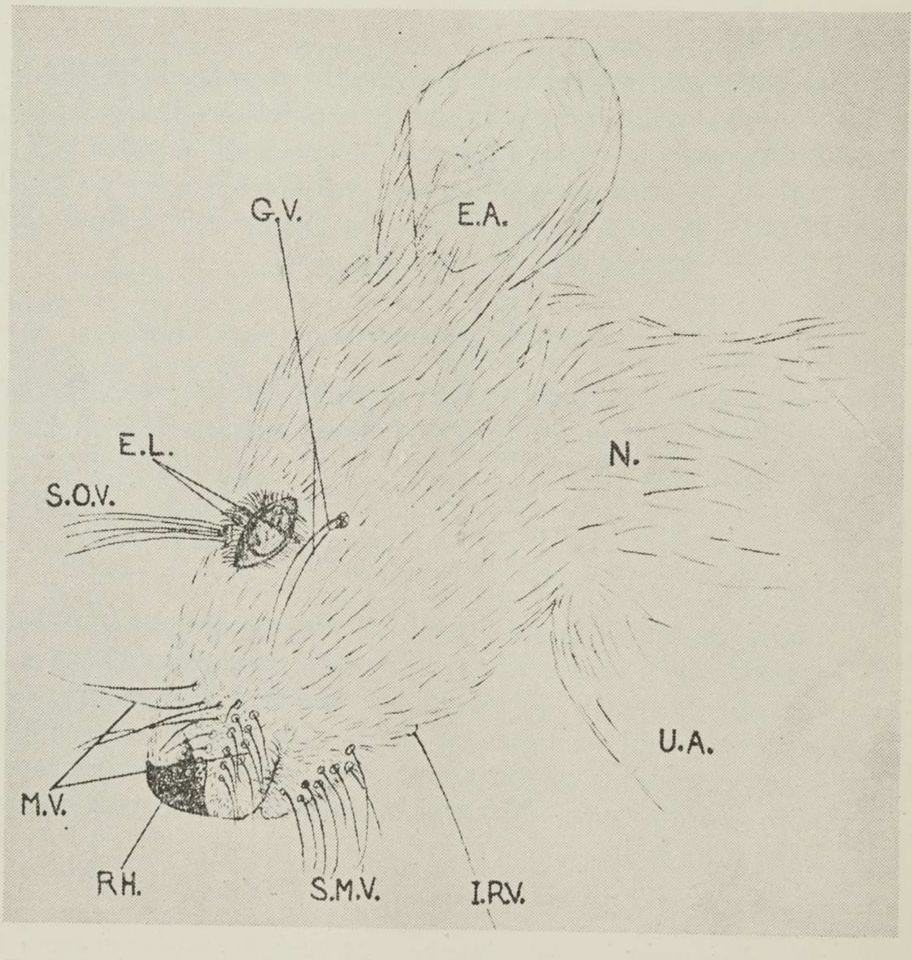
Head shaggy in appearance and may be more conical than the heads of larger macropods. (See suggested differences in relative lengths and breadth of head of *M. eugenii* and *S. brachyurus*. From region of maximum width, between eyes and ears, it tapers rapidly and uniformly to rhinarium. Profile from rhinarium to ears fairly flat; there is no convexity between the eyes (supra-orbital or frontal regions).

The interorbital region of two *skulls* examined is, in fact, slightly concave. In keeping with this uniform tapering, the muzzle is not abruptly truncated but has a rather rounded tip (see pl. I and text fig. 3).

c. Rhinarium (text fig. 4).

Rhinarium dark brown or black, relatively large and well formed and distinctly marked off from rest of hair-covered muzzle. It is up to 17 mm. in depth, 13 mm. in breadth and extends about 7 mm. along muzzle. It extends slightly on to dorsal surface of face, whereas in *M. eugenii* it does not. Rhinarium of *M. eugenii*, smaller.

Rhinarium of quokka has a small, rounded, median projection from its caudal and dorsal margin. This projection, which is directed caudad along muzzle, is about 1 mm. long and 3 to 4 mm. wide at its base, where it joins the rest of the rhinarium. Nostrils crescentic in outline; there is a median cleft extending



Text fig. 3.—**S. brachyurus.** Lateral view of head. ¾ natural size. E.—eye; E.A.—external ear; E.L.—eyelashes; G.V.—genal vibrissae; I.R.V.—interramal vibrissa; M.V.—mystical vibrissae; N.—neck; RH.—rhinarium; S.M.V.—sub-mental vibrissae; S.O.V.—supra orbital vibrissae; U.A.—upper arm.

about half way up rhinarium. Cleft widens towards the oral margin of upper lip, exposing anterior upper pair of incisors. Rhinarium continuous with upper lip by way of two narrow bands of naked skin, separated by median rhinal cleft.

Rhinarium hairless, its surface granular or tessellated; tesserae largest in middle line and diminish in size towards margins of rhinarium.

d. Eye. (text fig. 1).

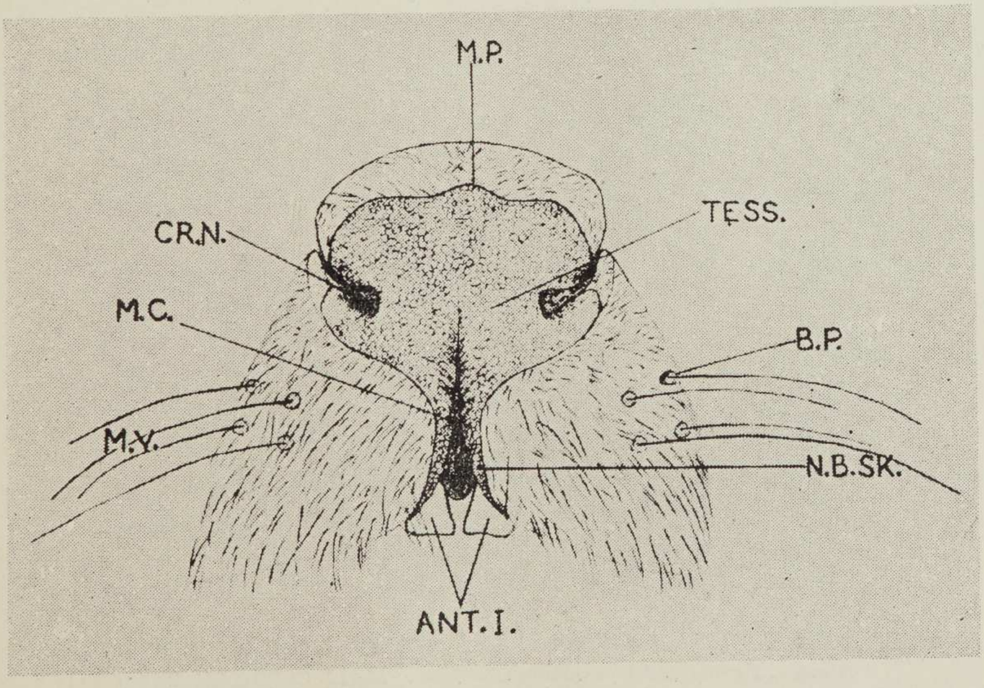
Each eye is 11 to 15 m.m. long, measured from canthus to canthus. Iris dull dark brown, eyelashes black, those of upper eyelid being the longer, their maximum length being 10 mm.

e. External ear (text fig. 5).

Inner and outer surfaces of external ear covered with red hairs; those of inner surface softer and finer than those of outer.

The short and rounded form of the external ears of *Setonix* is strikingly different from the elongate ear characteristic of the genus *Macropus* (Wood Jones, 1924a, p. 234, and also my suggested differences in relative length and breadth of ear of *M. eugenii* and *S. brachyurus*, p. 71).

Following Cunningham (1937, p. 101) and Wood Jones (1923, p. 7 and fig. 2), the concha shows a well developed tragus, an antitragus and an antihelix. Antitragus not as well developed as tragus, which is partly separated from rest of cephalic (dorsal) part of helix by a small notch. Between tragus and antitragus is a larger notch. Antihelix is a low ridge within concha, near,



Text fig. 4.—**S. brachyurus.**. Rhinarium shown in relation to surrounding hair-clad muzzle. 2 x natural size.

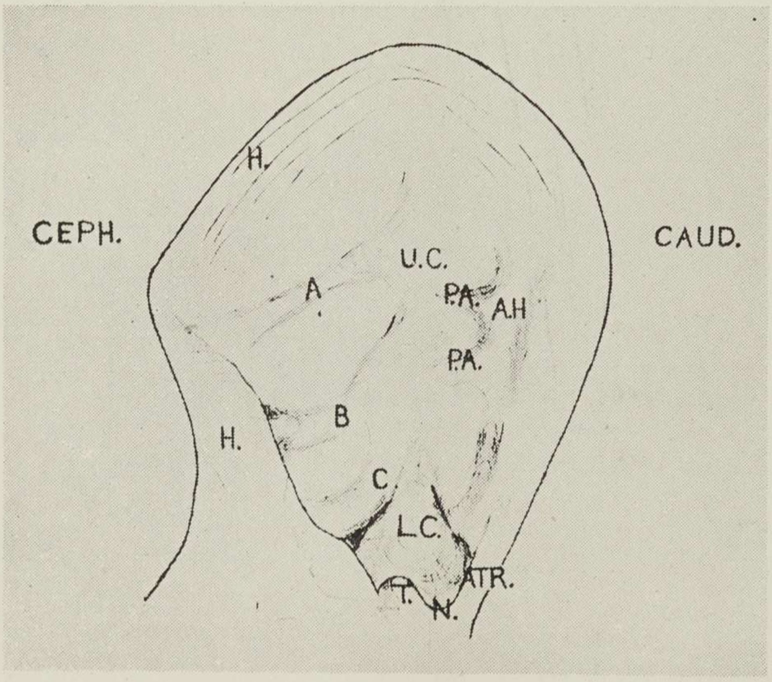
ANT. 1—1st pair of upper incisors; B.P.—basal papilla of a mystical vibrissa; CR.N.—crescentic nostrils; M.C.—median cleft of rhinarium; M.P.—median projection of rhinarium; M.V.—mystical vibrissa; N.B.SK.—narrow band of naked skin between rhinarium and upper lip; TESS.—tesserae covering rhinarium.

and approximately following outline of caudal (ventral) margin of external ear. As secondary processes of the anti-helix there are at least two processi antithelicis, which are short and run from the antihelix towards the cephalic margin of ear; they terminate in the region of the mid-longitudinal axis of ear. There are also three other secondary processes within the concha. Two of these (B and C in text fig. 5) are well developed and lie in the lower cephalic half of concha. At their cephalic end they appear to merge into the helix: towards their caudal ends they become low and, fanning out, merge into the general inner surface of the concha; both approach the processi antihelicis, the low caudal end of B being closer to them than that of C.

The third secondary process (A in text fig. 5) is a low, ill defined ridge, variable in the amount of its development. It loses its identity cephalad before reaching the helix; caudad it fans out over surface of concha, so that in part it tends to be continuous with caudal end of B. It does not approach the antihelix or its processi as closely as does B.

Though A, B, and C do not appear to arise in the adult from the antihelix, they may possibly be regarded as processi antihelicis.

There is no bursa developed in the caudal margin of the helix.



Text fig. 5.—**S. brachyurus.** Left external ear showing processes developed within concha. Hair covering external ear omitted. 1½ x natural size.

A, B and C—see p. 76; A.H.—antihelix; ATR.—antitragus; CAUD.—caudal (ventral) margin; CEPH.—cephalic (dorsal) margin; H.—helix; L.C.—lower part of concha leading to external auditory meatus; N.—notch separating tragus from helix; P.A.—processi antihelicis; T.—tragus U.C.—upper part of concha.

f. Facial vibrissae (text figs. 3 and 4).

All groups of facial vibrissae, which are regarded by Wood Jones (1923, p. 7) as typical of mammals, represented, though some are better developed than others. Vibrissae generally distinctly thicker and stiffer than other non-sensory hairs covering head. Each arises from a basal, grey coloured, papilla about 0.5 mm. in diameter.

It seems that, in keeping with the general darker colour of hair of upper surfaces of body as contrasted with the lighter coloured hair of lower surfaces, the vibrissae of dorsal and dorso-lateral aspects of head are dark brown, those of ventro-lateral and ventral aspects are lighter coloured, so that, for instance, the inter-ramal vibrissae is almost silver grey.

i. Mystical set.—Most extensive and best developed set. It is quite distinct, being on either side of tip of muzzle, occupying an area about 10 m.m. square, of which the cephalic margin is about 10 mm. from tip of muzzle, and the upper (dorsal) margin about 10 mm. below dorsal surface of muzzle. Each vibrissa directed laterally from its point of origin. There are four longitudinal rows of papillae with their associated vibrissae. The rows decrease in definition dorsad, and above the last distinct row, there may be additional unorientated papillae with vibrissae arising from them. The vibrissae, which reach a maximum length of about 25 mm., are dark brown or black in the upper rows, and of a lighter shade in the lower (oral) rows.

ii. Submental set.—This is a well developed, distinct set on the right and left margins of lower jaw. Vibrissae dispersed over an area about 10 mm. long and 5 mm. deep, the cephalic margin or which is about 10 mm. from tip of lower jaw; they are directed down and out from their points of origin, and number about nine in each area. They are a light shade of brown and reach a maximum length of about 15 mm., being the shortest vibrissae of face.

iii. Interramal set.—This is unpaired and seems very poorly developed, for it was seen only in two of the six specimens examined. In the two—an adult male and an adult female—there is a single vibrissa arising from a distinct papilla situated in the middle line of lower jaw and about 25 mm. from its tip. Vibrissa is almost silver grey, directed downwards from its point of origin, reaching a length in the male of 30 mm. and in the female of 20 mm.

iv. Supraorbital set.—This is small but distinct, the basal papillae being packed close together to form, as it were, one large papilla about 3 mm. long and 2 mm. wide. The set is on each side of head about 3 mm. above eye and 2 mm. behind its posterior canthus. Vibrissae, about four in number, dark brown or black and directed out and up from their basal papillae. Maximum length about 25 mm.

v. Genal set.—This is a small set, and, as with the supraorbitals, its basal papillae are packed closely together so as to give the impression that there is but one large papilla, about 2 mm. in diameter on which smaller papillae are superimposed. The set lies on either side of head, about 10 mm. below and 4 mm. behind posterior canthus of eye. It has two or three strongly developed vibrissae, which have a maximum length of about 35 mm. Each is dark brown or black and is directed out and slightly back from its basal papilla.

2. *Hairs of thorax.*

Shoulders covered with rufous hairs and a smaller number of gray and dark brown (black) hairs. Rufous area of shoulder roughly triangular (isosceles) in shape, apex of triangle pointing caudad and base of triangle stretching transversely across shoulder from forelimb to forelimb. Extent of this rufous area of shoulder varies, if not with sex, then with condition of animal; its apex may be half way along dorsal aspect of body.

Dorsal surface of thorax therefore slightly rufous; lateral surfaces grizzled grey.

3. *Fore limb.*

a. Hair.

Because of lateral extension of rufous area of shoulder, hairs covering the outer surfaces of upper arm and forearm (animal orientated as in pl. I) largely light rufous with a smaller number of slate-grey and brown hairs mixed with them. Inner surfaces, as with all ventral aspect of body, light (silver) grey. Hair of forearm becomes shorter towards its distal end. Back of hand covered for about 10 mm. with short, dark brown hairs, which are directed distad and extend to tips of fingers. There is a prolongation of these dark brown hairs proximad along the postaxial side of forearm for about 10 mm.

b. Vibrissae (text fig. 6).

Of the three possible vibrissal groups of the forelimb only one, the ulnar carpal, is developed and has but one papilla and vibrissa. Papilla well developed, being raised about 0.5 mm. above surface of surrounding skin, and being about 1 mm. across at its base. Vibrissa poorly developed, being of same colour and about same length (15 mm.) as surrounding hairs of forelimb.

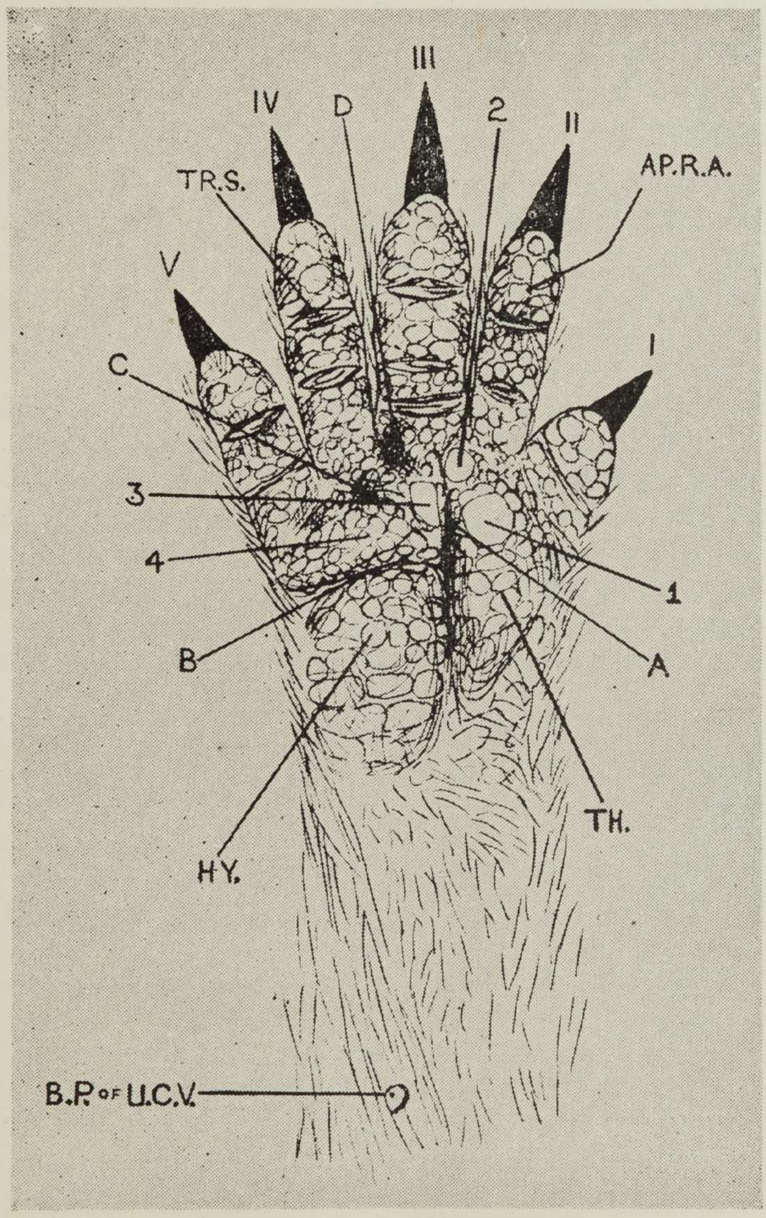
In palmar view of hand, the papilla of ulnar-carpal vibrissa is seen just on post-axial side of axis of forelimb and about 15 mm. from proximal end of hypothenar pad of manus; i.e. with the animal orientated as in pl. I, the papilla is on inner caudal margin of forelimb.

c. Hand (text figs. 6 and 7).

Hand has five digits, each tipped with a dark brown claw. Digital formula is 3> 4> 2> 5> 1.

Claws all sharp-pointed, and, when viewed from the side, are of crescentic outline (text fig. 7a). They are shorter and broader than those of a specimen of *Bettongia penicillata* which I have examined.

Third finger longer than its claw (see Tables I, III and V); other fingers are also longer than their claws, whereas in the specimen of *B. penicillata* the third finger is shorter than its claw. Apart from differences in size between the claws of *S. brachyurus* and *B. penicillata,* they differ in their transverse



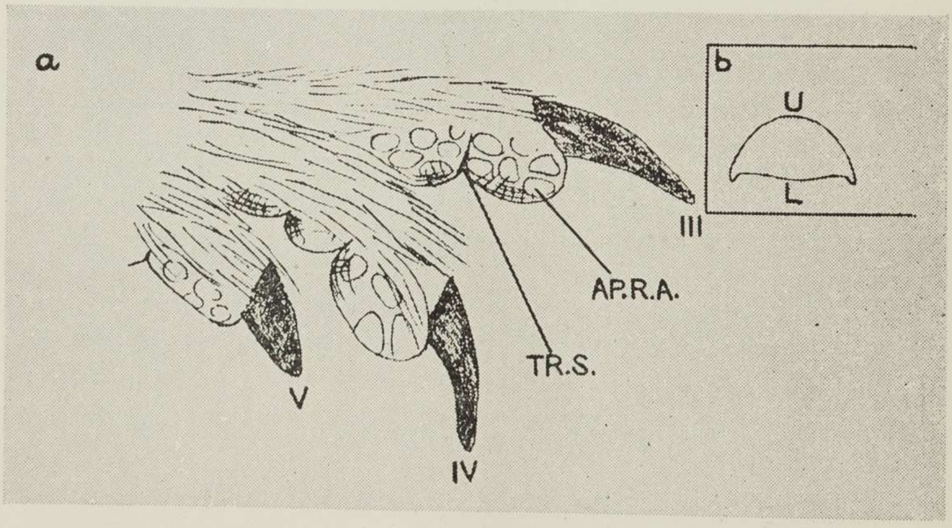
Text fig. 6.—**S. brachyurus.** Right hand, palmar surface. 2 x natural size.

I-V—fingers tipped with claws; 1-4—region of apices of 1st, 2nd, 3rd and 4th inter-digital pads. A and B —see p. 80; AP.R.A.—apical raised area; B.P. of U.C.V.—basal papilla of ulnar carpal vibrissa; C and D—see p. 80; HY.—hypothenar pad; TH.—thenar pad; TR.S.—transverse sulcus (depressed area of finger.

sections: in *Setonix* the claws have a convex upper and a plane, or slightly concave lower surface (text fig. 7b); in *B. penicillata* the claws are almost cylindrical in section, the upper surface being strongly convex, the lower surface, while not as convex, is certainly not plane or concave.

It is of interest to note that, in the specimen of *B. penicillata* examined, the skin of the palms, and the claws tipping the fingers, are of a dirty white colour. The palmar surface of the hand of *Setonix* is hairless. Its skin, which, like the claws is of a dark, dirty brown colour (cf. *B. pencillata*), is granulated. Unlike the granules on the palm of *Trichosurus vulpecula* (Wood Jones, 1924a, p. 197), the granules of *Setonix* are not arranged in lines and so do not give the palm a striated appearance.

Four sulci differentiate the palmar surface into a number of pads. The most extensive of these sulci (marked A in text fig. 6) is almost continuous with long axis of third finger. It runs from proximal to distal end of palm, turning slightly to the pre-axial side a few millimetres before it terminates between second and third fingers; it loses its definition slightly towards distal end. From post-axial margin of manus, at base of fifth finger, a sulcus (B in text fig. 6) extends transversely across palm to the longitudinal sulcus (A). From between the fourth and fifth and the third and fourth fingers, smaller sulci, (C and D in text fig. 6) run obliquely across palm towards longitudinal sulcus, losing their definition as they approach it. By references to these sulci, pads on the palm, which may be representatives of the typical palmar pads mentioned by Wood Jones (1923,



Text fig. 7a.—**S. brachyurus.** Lateral (post axial) view of fingers III-V of right hand. 2 x natural size. Abbreviations—see text fig. 6.

Text fig. 7b.—**S. brachyurus.** Outline of transverse section through through base of claw of 3rd finger. About 2½ x natural size. U.—upper (convex) surface of claw; L.—lower palmar (concave) surface of claw.

p. 8), can be described. In proximal post-axial half of palm is the well developed hypothenar pad, which is bounded on its pre-axial margin by promixal part of longitudinal sulcus.

Between sulci C and B, marking distal end of hypothenar pad, is a raised area which may be interdigital pad 4. Between C and D is a second raised area which may be interdigital pad 3. Occupying the whole preaxial margin of palm is a long, raised area, the proximal half to two-thirds of which is probably made up of thenar pad; the rest is probably formed of coalesced first and second interdigital pads.

Granules of palm appear to be small and strongly differentiated in the sulci. Towards apex of each palmar pad the granules are larger, but have not such definite outlines as those within, and on the margins, of the sulci.

In addition, towards proximal end of thenar and hypothenar pads, the granules, as they approach the general undifferentiated epidermis of forearm are larger, but poorly defined. On the long raised area of pre-axial side of palm of an adult female and near base of its first finger, was an area of smooth skin about 2 mm. square. From its position it may represent the true position of the first interdigital pad. A second slightly smaller smooth area lay at base of cleft between second and third fingers—this may mark the true postion of the apex of the second interdigital pad. A third smooth area of about the same size as the second occurred on longitudinal axis of manus, at base of third finger but proximal to the second smooth area. It may be the true position of the apex of third interdigital pad.

Alternatively, however, these three smooth areas may merely be parts of the palm which, in this particular animal, were subject to considerable wear and where the outlines of granules have been completely lost. However, on the distinctly granular hand of the larger and more advanced of the two pouch embryos, particularly large granules occurred, one near the base of second finger, another at base of the third, and another near base of cleft between second and third fingers. These appeared to correspond in position to the smooth areas occurring on palm of adult female just described.

Lower surface of fingers hairless and covered with the same dirty, dark brown granulated skin as palm. No distinct apical pads, but transverse sulci, corresponding to the joints between adjacent phalanges, divide each finger into raised and depressed areas, the raised being larger than the depressed and corresponding to each phalanx of a finger. Thus an apparent apical pad is produced at the end of each finger, but it does not seem to be the same as a true apical pad.

4. *Hairs of dorsal surface of abdomen.*

Hairs of dorsal aspect of abdomen, caudal to rufous area of shoulders, annulated. They vary considerably in length, ranging from

28 to 40 millimetres; proximal three-fifths of each hair dark grey, 'succeeded by a pale yellow or pale rufous band one-fifth of length of hair; rest of hair dark brown. Mixed with these annulated hairs are a few long (45 mm.) uniformly dark brown (black) hairs. They are confined to dorsal surface of body and do not occur on lateral surfaces, nor on limbs.

Though mixed with dark brown and rufous colours, the dominant colour of back, caudal to the rufous area of shoulder, is dark grizzled grey.

Within an arc with radius of 40 mm. of base of tail on dorsal and ventral surfaces of body, and also on dorsal (superior) and ventral (inferior) surfaces of the first 30 mm. of tail, the hair is slightly differentiated from the surrounding fur: owing to each of the three bands of colour on each hair being lighter in shade than the corresponding bands of hairs covering caudal dorsal surface of body, the hairs of this small area are, as a whole, of a lighter shade: in addition they are slightly curled.

5. *Hind limb.*

a. Hair.

Hairs of thigh and leg annulated in the same proportions and colours as those of dorsal abdominal surface.

b. Vibrissae.

No trace of typical mammalian calcaneal set for hind limb could be found in *Setonix.*

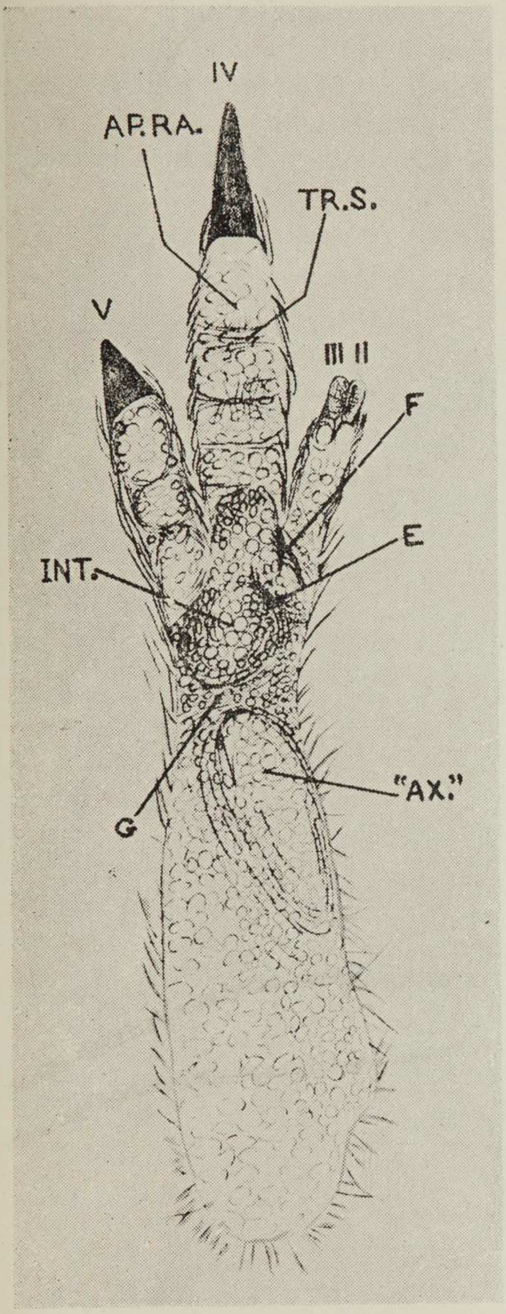
c. Foot (text figs. 8 and 9).

Foot not long and slender as in *B. penicillata,* but relatively shorter and broader. Four toes, the second and third being bound together to form a syndactylous toe. Hallux missing.

Digital formula is $4 > 5 > \widetilde{3.2}$.

Each toe is tipped with a dark brown claw. Hairs which cover dorsal surface of foot directed distad and extend to a point about 5mm. from base of claw. Because of their length they cover the tip of each toe and proximal part of each claw. They appear to be coarser than hairs covering leg and thigh. Hairs of margins of foot on the preaxial side as far as tip of syndactylous toe, and on the post axial side to base of fifth toe, uniformly grey and not annulated. Rest of dorsal surface of foot covered with dark brown hairs, which are also individually of uniform colour and not annulated. Plantar surface of foot hairless and marginal hairs of dorsal surface show no tendency to encroach on it; this contrasts with *B. penicillata* and, to a lesser extent, with *M. eugenii,* which show encroachment on the plantar surface of fourth and fifth toes and of base of the syndactylous and fifth toes.

Fourth toe, forming axis of foot, slightly less than one-third the length of foot. There is apparently no significant difference between the ratio, length of foot: length of fourth toe in *S. brachyurus* and *M. eugenii;* in the former the mean of this



Text fig. 8.—**S. brachyurus.** Plantar surface of right foot. Natural size.

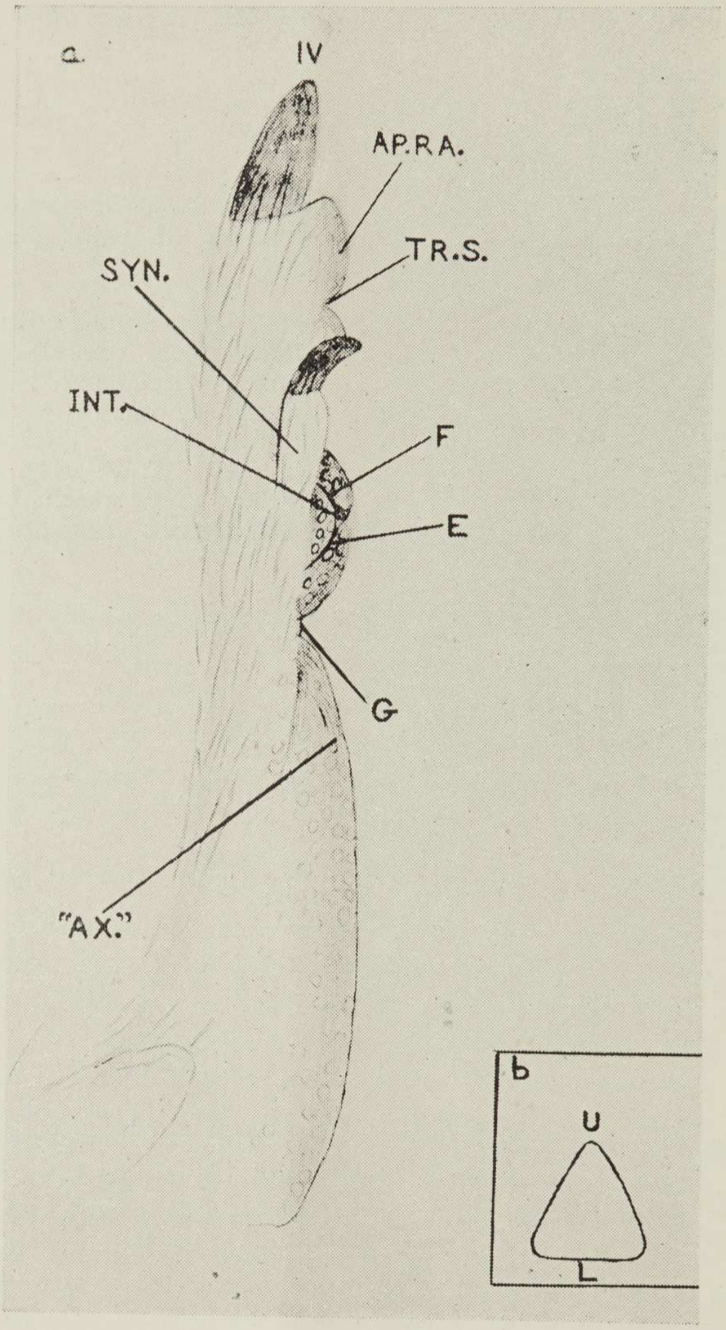
II-V—toes tipped with claws; AP.-RA.—apical (distal) raised area; "AX."—"axial pad"; E and F—see p. 85; G—see p. 85 INT.—inter-digital pad; TR.S.—transverse sulcus; W.A.—worn area (post axial) over which granules lose definiteness of outline.

ratio for six animals was 1:0.32, and in the single specimen of *M. eugenii,* was 1:0.31. Finlayson (1932, p. 156) in describing the pes of *Caloprymnus campestris,* states that the ratio of pes to fourth toe is 1:0.46, which he considers much higher than that shown by the Macropodinae. It seems then that *S. brachyurus* and *M. eugenii* may be typical of their sub-family in this respect.

Claw, which is short and pointed, is about half the length of fourth toe and is deep and broad at its proximal end where it joins the toe. It is triangular in transverse section (text fig. 9b), apex of triangle being uppermost.

Fifth toe is about half as long as fourth; its claw has the same shape as, but is slightly smaller than, that of the fourth.

Syndactylous toe bifurcates 2 or 3 mm. from its distal end. Each ramus of this bifurcation is tipped by a claw of shape very different from that of fourth or fifth toes, and is directed forward (text fig. 9a), This contrasts with *Caloprymnus campestris* in which each claw of the syndactylous toes is directed



Text fig. 9a.—**S. brachyurus.** Lateral (pre-axial) view of left foot. Natural size.

SYN.—syndactylous toe. Other abbreviations—see text fig. 8.

Text fig. 9b.—**S. brachyurus.** Outline of transverse section through base of claw of 4th toe. About 2½ x natural size.

U—upper (dorsal) surface of claw; L—lower (plantar) surface of claw.

upwards (Finlayson, 1932, p. 157 and fig. 3D). Each of these claws in *Setonix* is of the same shape, and, when viewed from the side, is of crescentic outline and has a convex dorsal and concave plantar surface. Convexity of second claw faces the preaxial, that of third faces the postaxial margin of foot; the concavities of plantar side face each other and consequently that of the second claw faces the postaxial, that of the third faces the preaxial side of foot.

Skin of plantar surface dark brown (as are the claws) and granular. Granules, which, like those of palm, are not arranged in lines, are usually 1 to 2 mm. in diameter. However, in certain regions, they are transversely elongated.

A single large interdigital pad on plantar surface. It is about 20 mm. long and extends from a point about 10 mm. proximal to base of fourth toe, to a point about 10 mm. along the latter. It occupies almost the full width of foot at base of toes. At proximal end of interdigital pad, and dividing plantar surface into proximal and distal portions, is a transverse depression (G in text figs. 8 and 9), 3 to 4 mm. across and widening considerably as it nears the preaxial margin of foot. Distal part of foot includes toes and interdigital pad; proximal part has a rather wide, plane surface, with granules of varying size and definition.

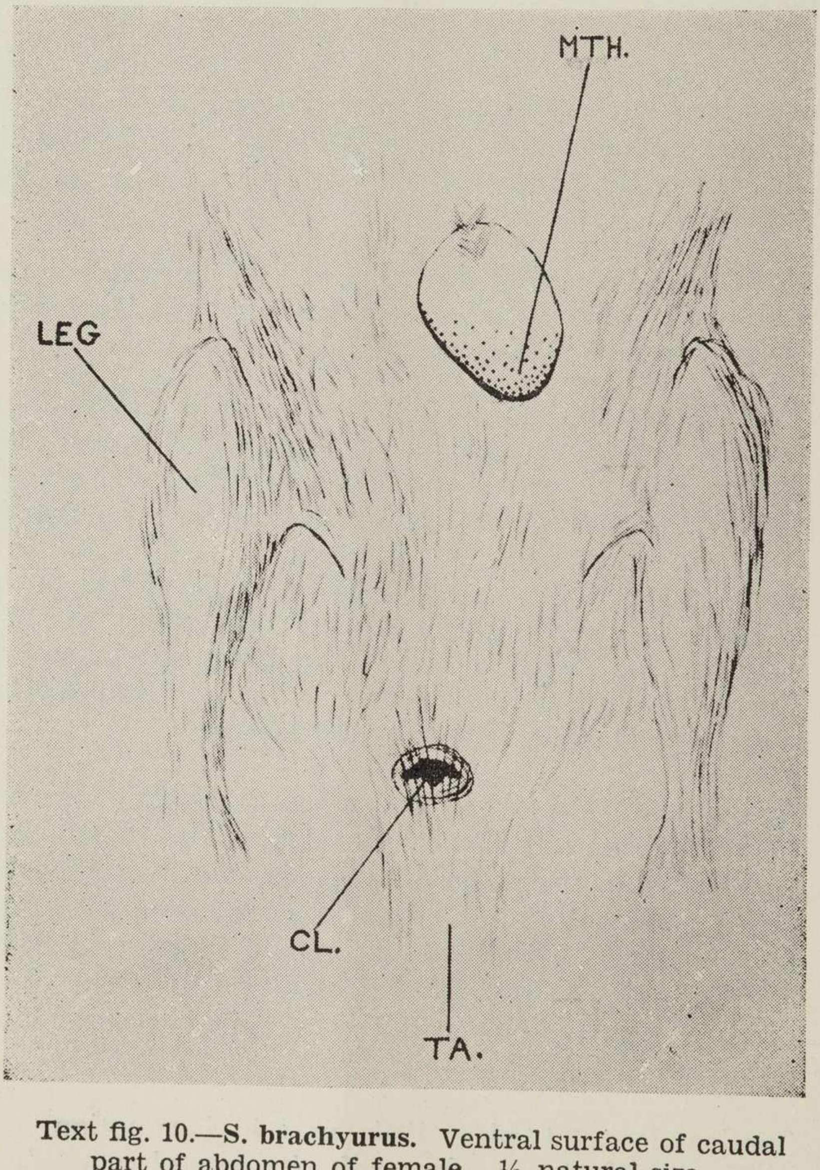
Granules at apex of interdigital pad enlarged, but have not such well defined outlines as granules of depressed areas of plantar surface, which are subject to less wear.

Two poorly developed sulci occur on interdigital pad. One, marked E in text figs. 8 and 9, is about 5 mm. long, rather shallow and wide, and runs from proximal and preaxial margin of pad obliquely across it towards cleft between fourth and fifth toes. The second, F in text figs. 8 and 9, is even more poorly developed, and extends from a point adjacent to cleft between the syndactylous and fourth toes, back towards distal end of E but fades out before reaching E. There are well developed creases between interdigital pad and bases of syndactylous, fourth, and fifth toes.

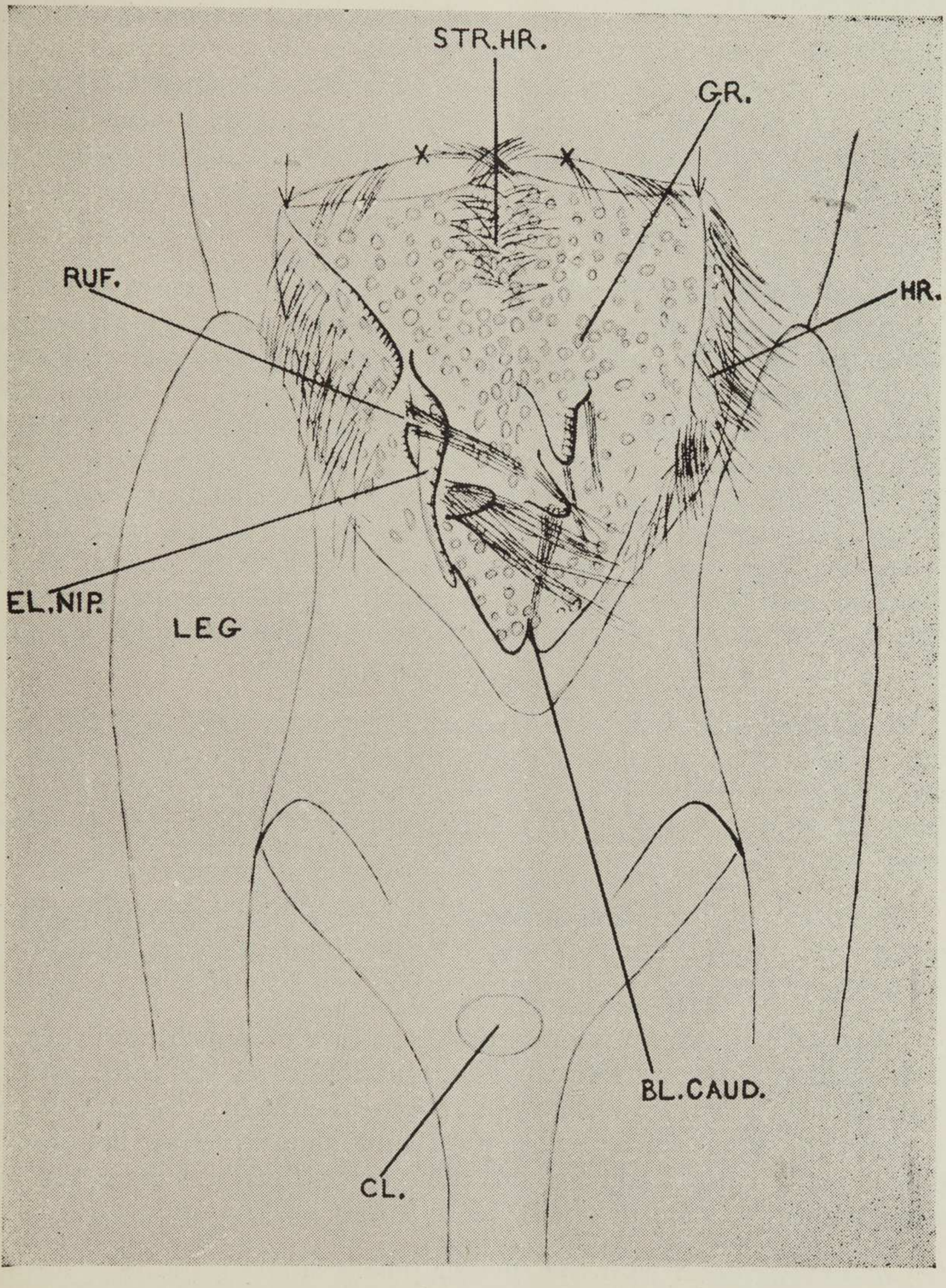
As with fingers, there are transverse sulci, corresponding to joints between adjacent phalanges, on the fourth and fifth toes which divide each toe into a number of relatively extensive raised and small depressed areas, each raised area corresponding to a phalanx. Distal raised areas of fourth and fifth toes have their granules transversely enlarged and flattened, the dimensions of the granules being 3 x 1 mm. Areas do not look like true apical pads.

Syndactylous toe plays little part in locomotion. Skin on its plantar surface therefore soft, its granules poorly developed. It has no well defined, deep transverse sulci like those of fourth and fifth toes. On proximal division of foot there seems to be a rather ill defined raised area (an "axial pad") running obliquely across its surface from middle line at the transverse depression, to preaxial margin of foot, about 40 mm. from its proximal end. Granules on this "axial pad" well defined, circular, and up to 2 m. in diameter. From it, towards the postaxial margin and proximal end of foot, the granules enlarge but lose definiteness of outline. Thus, on preaxial half of this proximal division, there is a raised area with well defined granules, and on postaxial half, extending towards the preaxial side at the proximal end of foot, is a flat area where the granules tend to be transversely enlarged, but are ill defined. This pattern of the proximal part of plantar surface suggests uneven wear and therefore an uneven gait. Careful examination of the "tracks" of the quokka might test this suggestion.

Granules covering proximal plantar surface of foot of *M. eugenii* did not show signs of this supposedly irregular wear.



Text fig. 10.—**S. brachyurus.** Ventral surface of caudal part of abdomen of female. ½ natural size. CL.—external opening of cloaca; MTH.—mouth of pouch; TA.—base of tail.



Text fig. 11.—**S. brachyurus.** Ventral surface of caudal part of abdomen of female. Pouch opened up by mid-longitudinal incision of its ventral wall and its lateral and ventral walls laid aside. All hair of surrounding ventral abdominal wall omitted. Natural size.

X-X—mouth of pouch; between arrows—maximum width; **BL. CAUD.**—blind caudal end of pouch; **CL.**—external opening of cloaca; **EL.NIP.**—elongate right cephalic nipple (see p. 88); **GR.**—granular inner surface of pouch; **HR.**—rufous hair of ventral and lateral inner wall of pouch; **RUF.**—long rufous hairs arising from base of nipple; **STR.HR.**—strip of hair extending short way down mid-dorsal inner wall of pouch; **TA**—base of tail.

6. *Hair of ventral surfaces of abdomen.*

Apart from two specialized areas round opening of pouch in female, and round and on scrotum in male, the ventral aspect of the body, including the inner surfaces of limbs, is of a silver grey colour which becomes a grizzly grey on flanks. Hairs become longer from neck towards tail, reaching a maximum of up to 35 mm. in pubic region. Each hair dark grey for its proximal two-thirds, changing to silver grey in distal third.

7. *Pouch* (text figs. 10 and 11).

Pouch situated on ventral surface of abdomen, between caudal end of thorax and the cloacal orifice. Its mouth, directed forwards, is surrounded by dark rufous hairs. It is roughly triangular in shape, though this, and its size, can probably be changed by muscular action. Pouch of one specimen, which contained the smaller poorly developed pouch embryo, had a mouth whose transverse diameter was 14 mm. the other diameter being 10 mm. In another specimen, which had no embryo, the corresponding measurements were 35 mm. and 24 mm. It may be, then, that when a young pouch embryo is present, the size of the mouth is reduced affording greater protection for the young animal. When empty, or when the pouch young is becoming independent of its parent, the mouth is possibly relaxed and larger.

In an area about 5 mm. wide round pouch opening, the hairs, each of which has a marked uniform rufous colour, are shorter and sparser than elsewhere on ventral surface. Thus pouch opening with its fringe of rufous hairs, is in marked contrast to the rest of ventral surface of body.

Pouch cavity is of maximum width just within the mouth. In one animal, the pouch of which was 60 mm. long, this maximum width was 45 mm. It tapers gradually to a blind caudal end.

Four nipples occur on inner dorsal surface of pouch, and they may be designated right and left cephalic, and right and left caudal nipples. Cephalic pair about 35 mm. from mouth of pouch. There is a space of about 15 mm. between the pairs and about 5 mm. between the cephalic and caudal nipples on each side; thus the four are comprised within an area of about 15 x 5 mm.

In the specimen with the smaller pouch embryo, the right cephalic nipple, to which the embryo was attached, was about 20 mm. long, the left cephalic was 10 mm., and the two caudal were 5 mm. long. Thus, when in use a nipple is a greatly elongated cone fitting far into mouth of embryo: those which are not in use are considerably shorter cones.

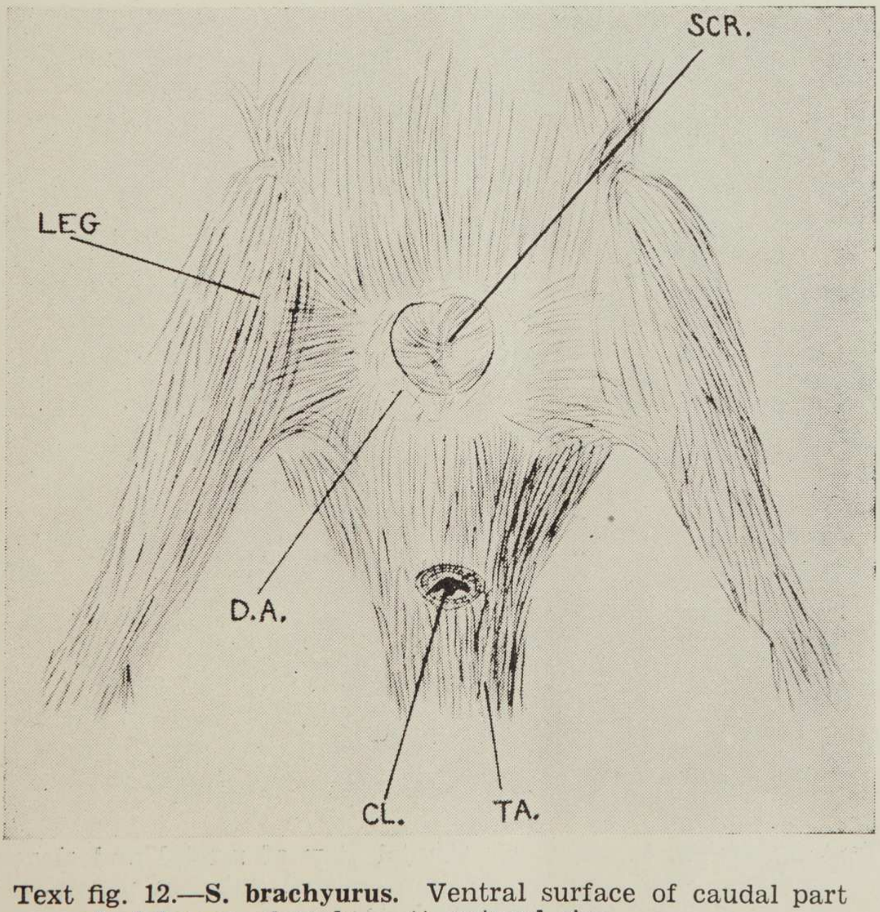
Inner surface of pouch has an uneven covering of rufous, silky hairs, the longest of which (up to 33 mm.) arise in clusters from base of each nipple. A strip covered with rufous hairs extends from the mouth for about 15 mm. down mid dorsal inner surface of pouch. Ventral inner wall of pouch fairly well covered with rufous hairs up to 15 mm. in length, but caudal wall has a very sparse covering of rufous hairs.

Skin lining pouch dirty white in colour and irregularly folded. These folds, largely longitudinal, may have been the result of preservation. Skin distinctly granular, the granules of internal dorsal surface being circular and about 1 mm. in diameter. Towards edge of dorsal wall and on lateral and ventral walls, they lose their definition.

8. *Scrotum* (text figs. 12 and 13).

Owing to a very complete descent of the testes the scrotum is conspicuous and pendulous. Its dorsal (superior) surface is about 4mm. below the ventral abdominal wall and supported by a neck or pedicle about 15 mm. wide and 5 mm. thick from front to back. Neck arises from a depression on ventral abdominal wall, which is about 5 mm. deep, 17 mm. wide (transverse) and 8 mm. long (cephalo-caudal). Surrounding this depression, and therefore surrounding junction of neck with ventral body wall, is a circular area, about 30 mm. in diameter, which, being covered by very fine, silky, pale yellow or white hairs, contrasts markedly with surrounding abdominal surface. Although, in several preserved specimens, the hair covering scrotum was light grey, in a living male it was rufous or brown and contrasts with the silver grey of ventral surface of body.

Hairs of scrotum most abundant on ventral (inferior) surface and become sparser towards dorsal surface and pedicle. Dark grey pigment



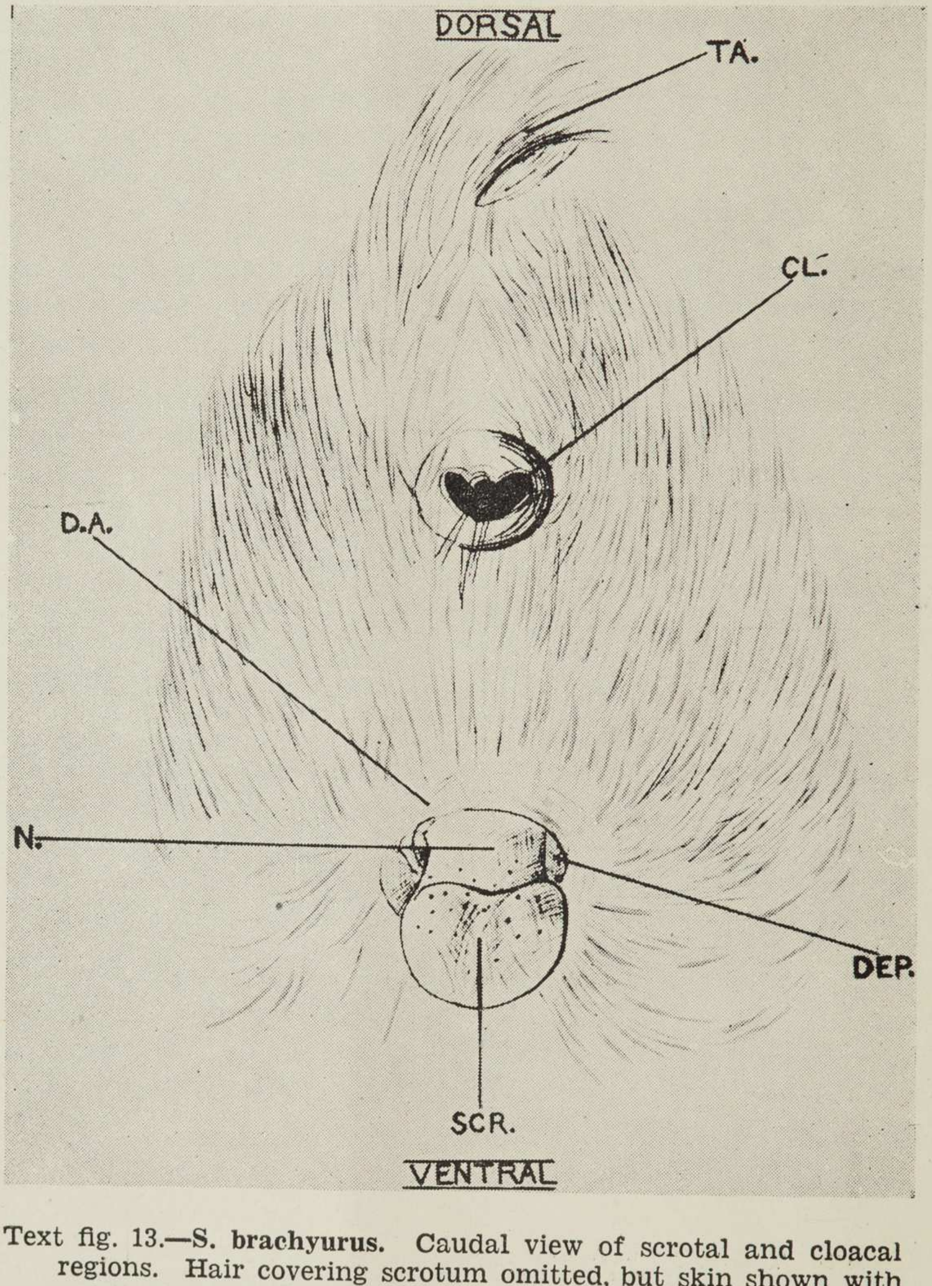
Text fig. 12.—**S. brachyurus.** Ventral surface of caudal part of abdomen of male. ½ natural size.

CL.—external opening of cloaca; D.A.—differentiated area around junction of neck of scrotum with ventral body wall; SCR—scrotum; TA—base of tail.

spots, less than 0.5 mm. across, occur on skin of scrotum, but are more apparent, and perhaps more numerous, on dorsal surface, where the covering of hair is thinner.

When viewed from ventral or from caudal aspects the scrotum is seen to be heart-shaped. It is from 20 to 25 mm. in cephalo-caudal length, from 15 to 20 mm. in transverse width and is about 15 mm. deep (i.e. from dorsal to ventral surfaces).

There is a depression, marking outline of testes, in the mid-cephalic, ventral, and caudal surfaces of scrotum.

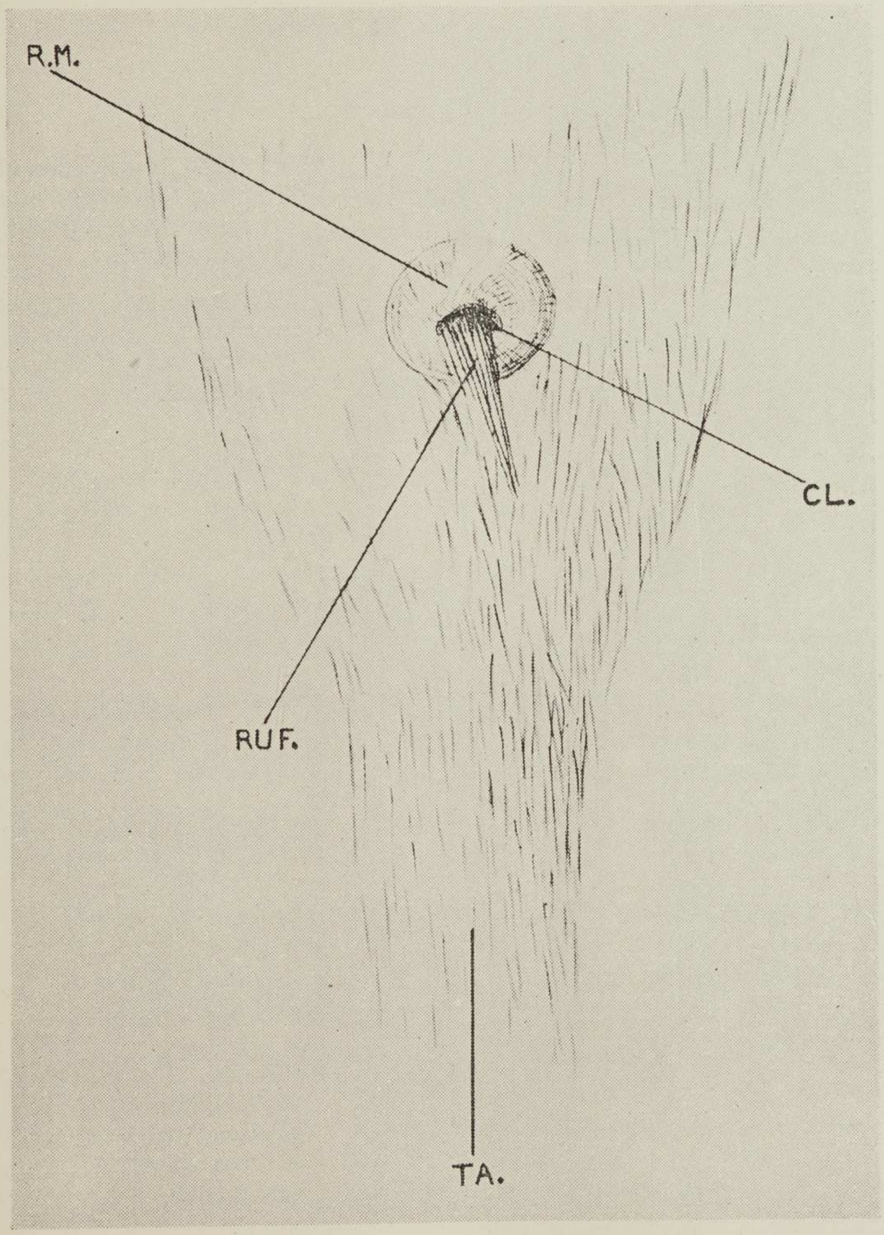


Text fig. 13.—**S. brachyurus.** Caudal view of scrotal and cloacal regions. Hair covering scrotum omitted, but skin shown with a few pigment spots. Natural size.

N.—neck (pedicle) of scrotum; DEP.—depression around base of neck where it joins ventral abdominal wall. Other abbreviations see text fig. 12.

9. *External opening of cloaca* (text figs. 13 and 14).

Margin of opening of cloaca, raised to form a flat-topped, circular ridge, sparsely covered with hairs, grey and about 5 mm. long on outer side of ridge, but becoming rufous and longer towards opening of cloaca. In both sexes on the inner (cloacal) side of ridge, almost from within cloaca itself, arise a number of long (20 mm.) rufous hairs. These may be cloacal vibrissae, described by Wood Jones (1920, p. 366) as occurring in pouch specimens and adults of *Trichosurus vulpecula.*

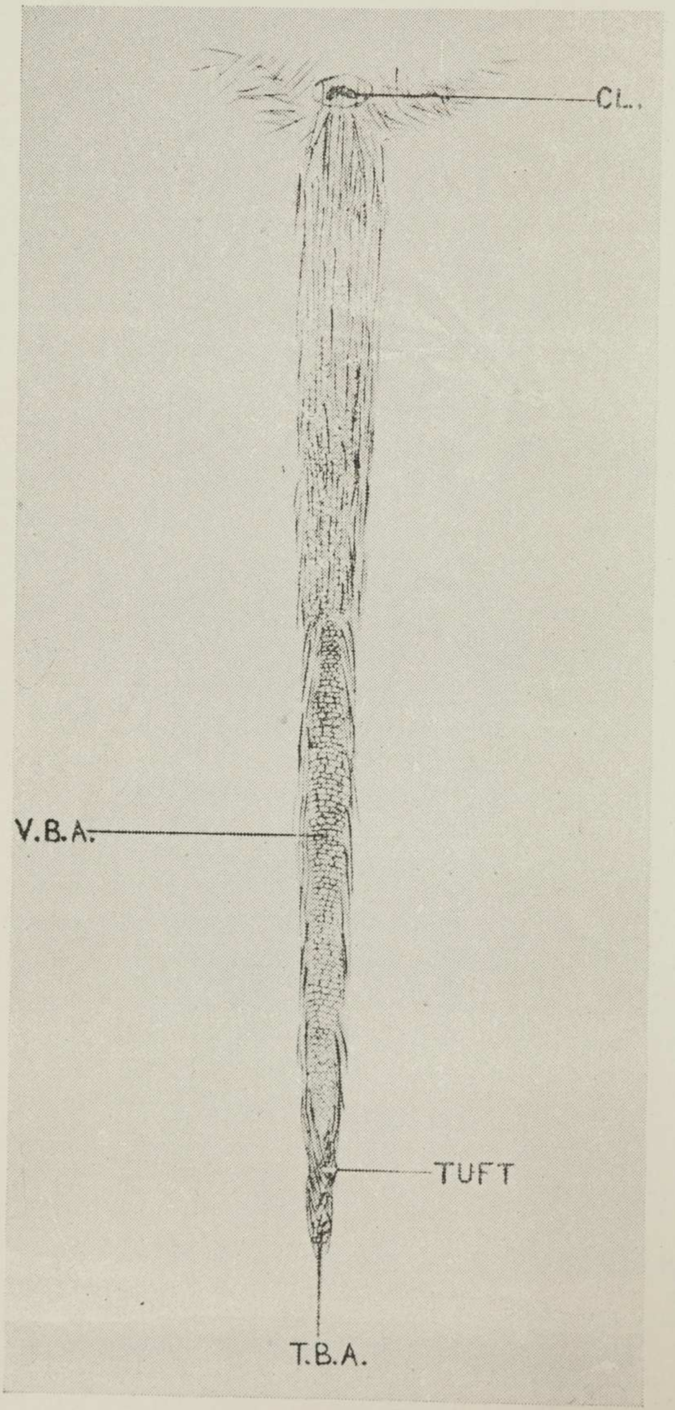


Text fig. 14.—**S. brachyurus.** Region of external opening of cloaca. Natural size
CL.—external opening of cloaca; R.M.—raised margins of cloaca (see p. 91); RUF.—long rufous hairs arising almost from within cloaca; TA.—base of tail.

10. *Tail* (text figs. 15 and 16).

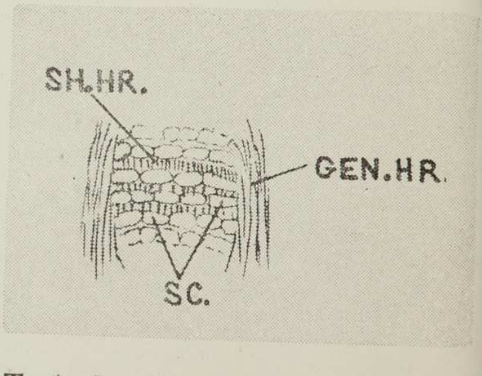
The fact that the tail of *Setonix* is short has been mentioned on p. 60 of the "Introduction" and on pp. 71 and 73 of the "Examination of Measurements," where it is suggested as being relatively shorter than that of *M. eugenii.*

Except for its first 40 mm. (see p. 82 of "Externals"), tail sparsely covered with short hairs, which are directed toward its tip and the scaly skin of tail becomes very obvious. Hairs of dorsal (superior) surface of tail banded. Proximal and distal bands brown, middle one pale rufous. Hair of lateral surfaces of tail grey and on ventral (inferior) surface silver grey or white, in conformity with general silver grey colour of ventral surface of body.



Text fig. 15—**S. brachyurus.** Ventral (inferior) surface of tail showing scaly epidermis. ½ natural size.

CL.—external opening of cloaca; T.B.A. — terminal bare area; V.B.A.—ventral bare area.



Text fig. 16.—**S. brachyurus.** Enlargement of portion of the ventral bare area of tail shown in fig. 15. 1½ x natural size.

GEN. HR.—general and relatively long hair covering most of tail; SC.—scales of tail; SH. HR.—short worn hair of ventral bare area.

In adults, distal half of ventral surface of tail apparently bare. Bare area is 100 mm. or more long and extends for the full width of ventral surface of tail. Ventral bare area does not extend to tip. However, in adults a very small terminal bare area about 5 mm. long and wide is developed.

Over the ventral bare area scales of skin become even more apparent than elsewhere on tail. Close examination shows that this area carries very short hairs, less than 1 mm. long, which arise between successive scales, as do the other longer hairs of tail.

An immature male specimen showed no terminal bare area and a very small ventral one about 30 mm. long. It seems then that this area gets larger as the animal grows older.

In contrast with *Setonix, M. eugenii* has a tail well covered with hair and showing no trace of a ventral bare area, although *Macropus* probably drags its tail on the ground when travelling slowly, as does *Setonix.*

Finlayson (1932, p. 160) after referring to the scaly epidermis of the tail of *Caloprymnus campestris,* says ". . . the under surface of the tail retains its dense covering through life, and its condition is exactly that of the typical wallabies and kangaroos." This, together with my observations on the tail of *M. eugenii,* accentuates the peculiarity of the ventral bare area of the tail of *Setonix.*

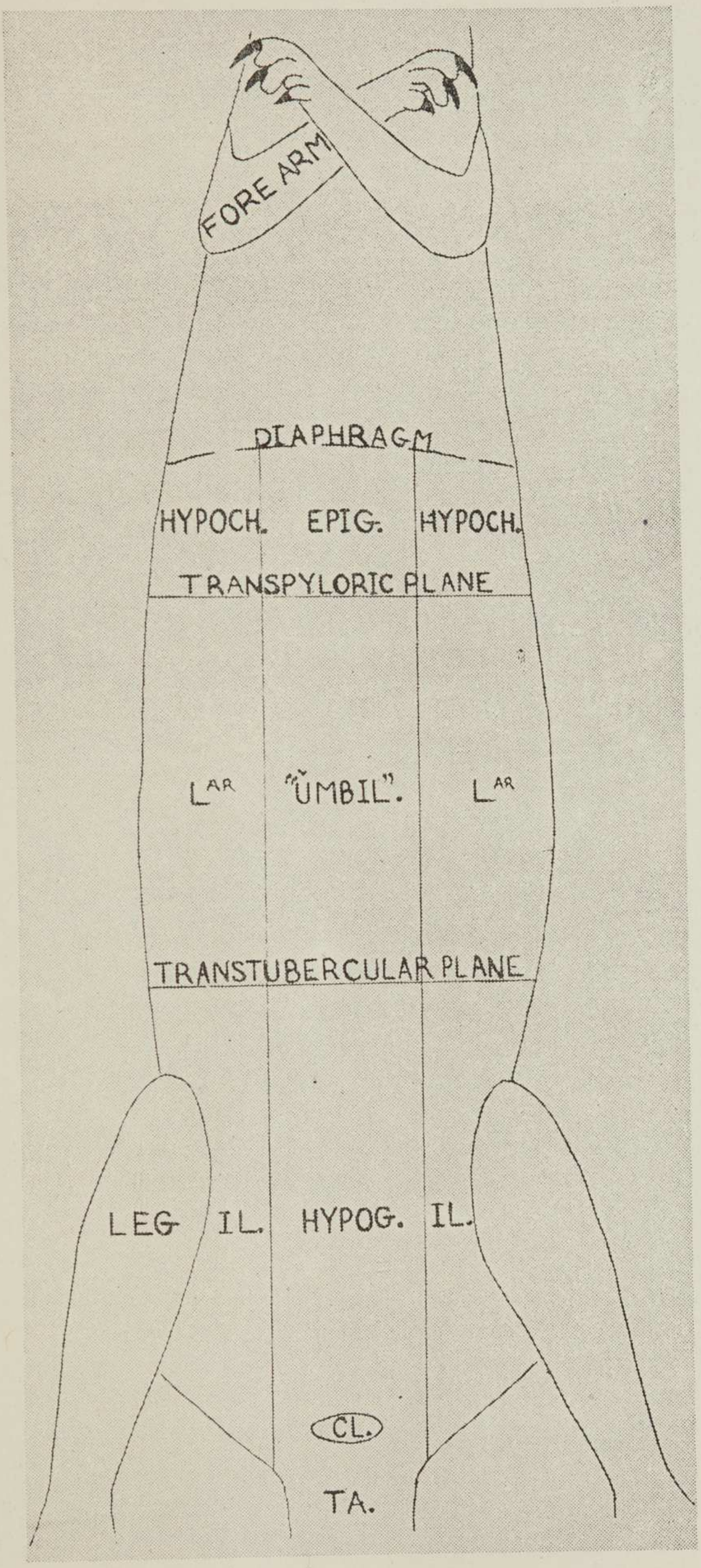
Hairs of greater part of dorsal surface of quokka's tail are up to 5 mm. long and, except for those on bare area, are shorter than those of ventral surface, which are up to 8 mm. long.

At distal end of tail the hairs of upper and lower surfaces become longer and form a small terminal tuft, the dorsal hairs contributing to which are up to 10 mm., the ventral up to 15 mm. in length.

In the immature male animal, whose ventral bare area is not very extensive, the distal 70 mm. of lower surface of tail are crested through elongation of the hairs, which are directed distad and towards middle line. In adults, owing to the development of ventral and terminal bare areas, this crest is reduced to a terminal tuft.

At proximal end , tail is flattened dorso-ventrad, so that transverse measurement (23 to 29 mm.) may exceed vertical by 5 mm. Dorso-ventral flattening is maintained for the first 40 mm; remaining distal part of tail grades from circular to laterally flattened section. Apart from the shortness of the tail, its most striking feature, noted by Waterhouse (1846, p. 162) is its scaly appearance, made more apparent by sparseness of hairy covering. Cephalo-caudal length of each scale, about 1 mm., and transverse width, about 3 mm. They are arranged in rings around tail and closely resemble those on tail of the white rat (*Mus rattus*), overlapping on all surfaces except lower, where their size and definiteness of outline is slightly reduced by wear.

Finlayson (1932, p. 160) and Gregory (1910, p. 146) mention the presence of scales on the tail of *Caloprymnus campestris* and *Petrogale* respectively.



Text fig. 17.—**S. brachyurus.** Ventral view of abdomen showing relative positions of planes dividing it up into various regions. (See Cunningham, 1937, p. 572; Gray, 1916, pp. 1068-9). About ½ natural size.

CL.—external opening of cloaca; EPIG.—epigastric region; HYPOCH.—right and left hypochondrium; HYPOG.—hypogastric region; IL.—right and left iliac region; LAR.—right and left lumbar region. TA.—base of tail; "UMBIL."—umbilical region.

In a well advanced, hair-clad, pouch embryo (*Macropus* sp.), the skin of tail showed creases but no scales. Skin of tail of *M. eugenii* appears to be merely lined and not scaly.

Gregory (1910, p. 146) in discussing the origin of hairs in mammals, attaches some importance to "the mingling of hairs and minute scales in the foetal *Dasypus* and in the tail of *Didelphis, Petrogale,* and many insectivores and rodents. The tail, being of little adaptive importance in the economy of many animals might be expected to retain in some instances very ancient hereditary characters."

I wonder whether the scales on the tail of *Setonix* would have been regarded (by Gregory) as a very ancient hereditary character, like those on the tail of *Petrogale* and other mammals, or whether, as seems more reasonable, the scales would be regarded as a secondary feature of the skin. I have been unable to examine the tail of *Petrogale* and so cannot assess the resemblance or differences between the condition of its tail and that of *Setonix.*

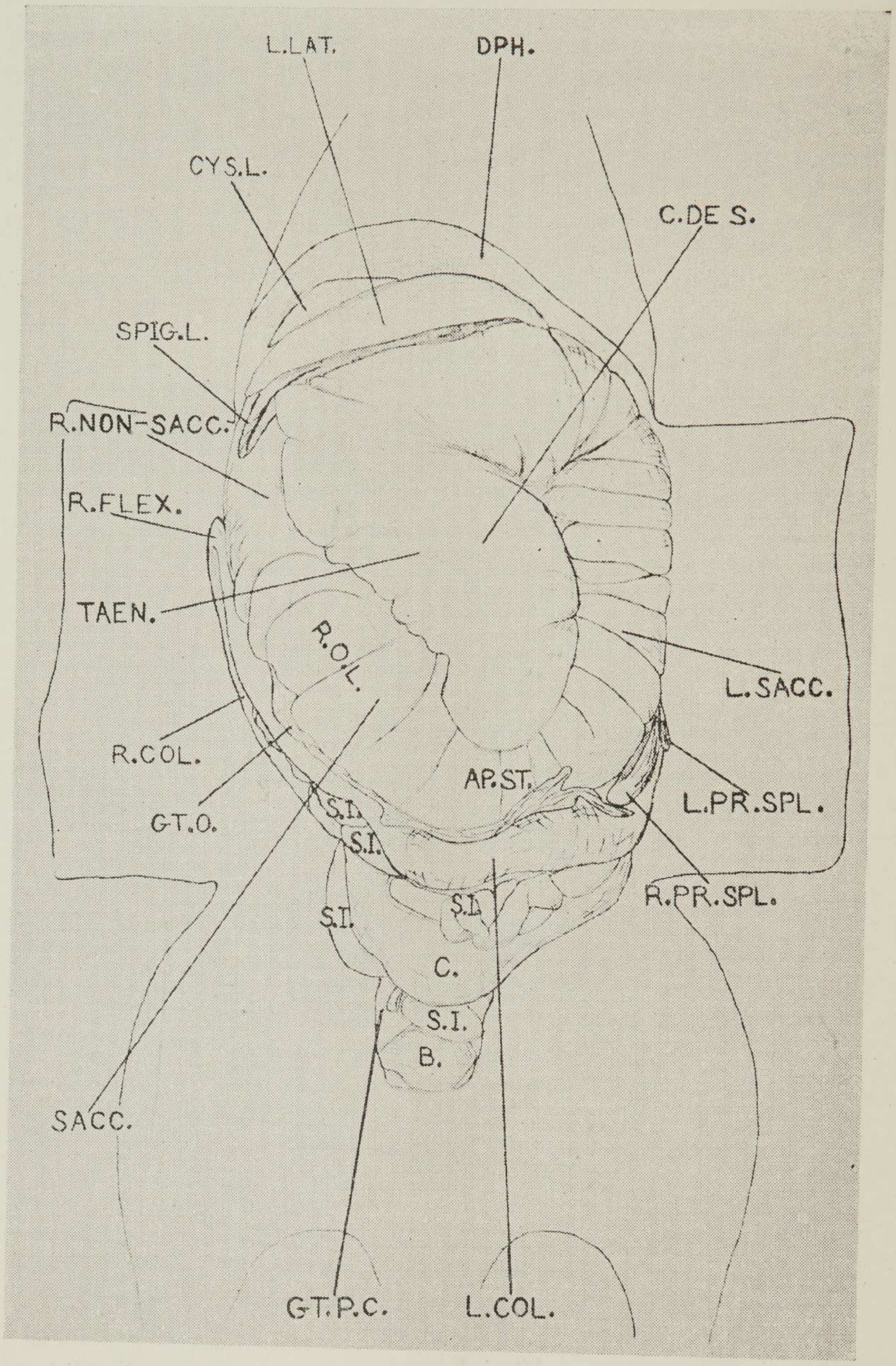
III.—LARGE INTESTINE.

A.—INTRODUCTION.

Cunningham (1937, pp. 593-4) uses the term large intestine to include caecum, colon and rectum. Mitchell appears to use the term *hind-gut* to cover colon and rectum, excluding caecum. Thus large intestine may be regarded as made up of a caecum and hind-gut.

In describing the large intestine of *Setonix* I have largely consulted Mitchell (1905, 1916), Beddard (1908), and Mackenzie (1918a and b; 1919). The descriptions of these authors is apparently based on the examination of fewer specimens of a given genus or species, than the seven of *Setonix* available to me. Mitchell and Beddard are concerned with the evolution of the pattern of the mammalian intestine, including the development of secondary loops of the colon (ansae coli), the formation of the cavo-duodenal and colico-duodenal ligaments and the homologies of the mammalian caecum. Beddard devotes more attention to secondary adhesions between remote portions of the intestine than does Mitchell, who concentrates more on the caecum and secondary loops of the intestine. They describe the intestinal pattern of most mammalian groups, including notes on that of macropods, other than *Setonix.*

Mackenzie (1918b) has described the gastro-intestinal tract of marsupials in detail. He devotes a section to macropods, of which he has examined a number of subgenera and species excluding *Setonix*. Unfortunately he gives no bibliographical list, so I cannot trace his terms. He either describes a completely new set of adhesions, or uses different names for those structures described by Mitchell and Beddard. The latter seems more reasonable, and accordingly I consider that his *mesial fold* is equivalent to the *colico-duodenal ligment* of Mitchell and Beddard, and his *right lateral* or *duodeno-mesocolic fold* is equivalent to their *cavo-duodenal ligment* (ligamentum cavoduodenale).



Text fig. 18a.—**S. brachyurus.** Ventral view of abdominal viscera *in situ*. Stomach considerably distended with food. ½ natural size.

AP.ST.—apex of stomach; B.—cephalic end of bladder; C.—caecum; C DE S.—cul-de-sac of cardiac extremity of stomach; CYS.L.—cystic (mesial) lobe of liver; DPH.—diaphragm; GT.O.—fold of greater omentum; GT.P.C.—greater (false) pelvic cavity; L.COL.—left (distal) colon; L.LAT.—left lateral lobe of liver (note accommodation of stomach); L.PR.SPL.—left (dorsal) process of spleen; L.SACC.—left sacculated (car-

However, Beddard is uncertain about the occurrence of the colico-duodenal ligment in marsupials and it is this which has caused my doubt as to whether the mesial fold is the colico-duodenal ligament. As I have followed Mackenzie for more detailed description of peritoneal adhesions in the colico-duodenal region, I have used his term (mesial fold) in this paper.

Klaatsch (1892) has described the evolution of the pattern of the intestine from Amphibia through Reptilia to the Mammalia. Within the mammals, he describes the complications of the colon involving the formation of secondary loops, and secondary adhesions between morphologically remote portions of the intestine. He devotes two sections to the description of the intestine of marsupials with notes on that of *Halmaturus*.

The colon of *S. brachyurus* appears to be much more simple than that of other macropods. Accordingly it can be divided into distinct and straight ascending, transverse and descending parts. Klaatsch (1892, p. 662) uses these terms with reference to the colon of *Halmaturus thetidis* (*Macropus thetidis*).

B.—CAECUM AND ILEO-CAECAL REGION.

1. *Caecum* (text figs. 18a, 19-23, 25).

a. Postion *in situ* (text fig. 18a).

Agreeing with what Mitchell (1916, p. 206) said of the caecum in mammals generally, in *S. brachyurus* it may be regarded as a forward continuation of hind-gut, the apex being directed parallel to ileum and towards proximal end of small intesine.

In *Setonix* the ileum and caecum meet at an angle that varies from individual to individual, but is always acute, being usually between 40° and 70°. This is in accord with what Mitchell (1905, p. 450 and fig 7) describes for *Bettongia penicillata* and infers for *Macropus bennetti,* when he says that the latter has a gut pattern essentially similar to that of *B. penicillata;* he does not specifically mention the angle between the ileum and caecum in *M. bennetti.*

From its proximal or basal end, at junction of colon and ileum in dorsal aspect of caudal part of right lumbar region, the caecum, running ventrad, usually extends obliquely to the left across the caudal portion of the abdomen. Its distal blind end is in mid-hypogastric region. The length of caecum, and consequently its right-to-left extent, varies from one specimen to another; in several specimens caecum extended no farther to

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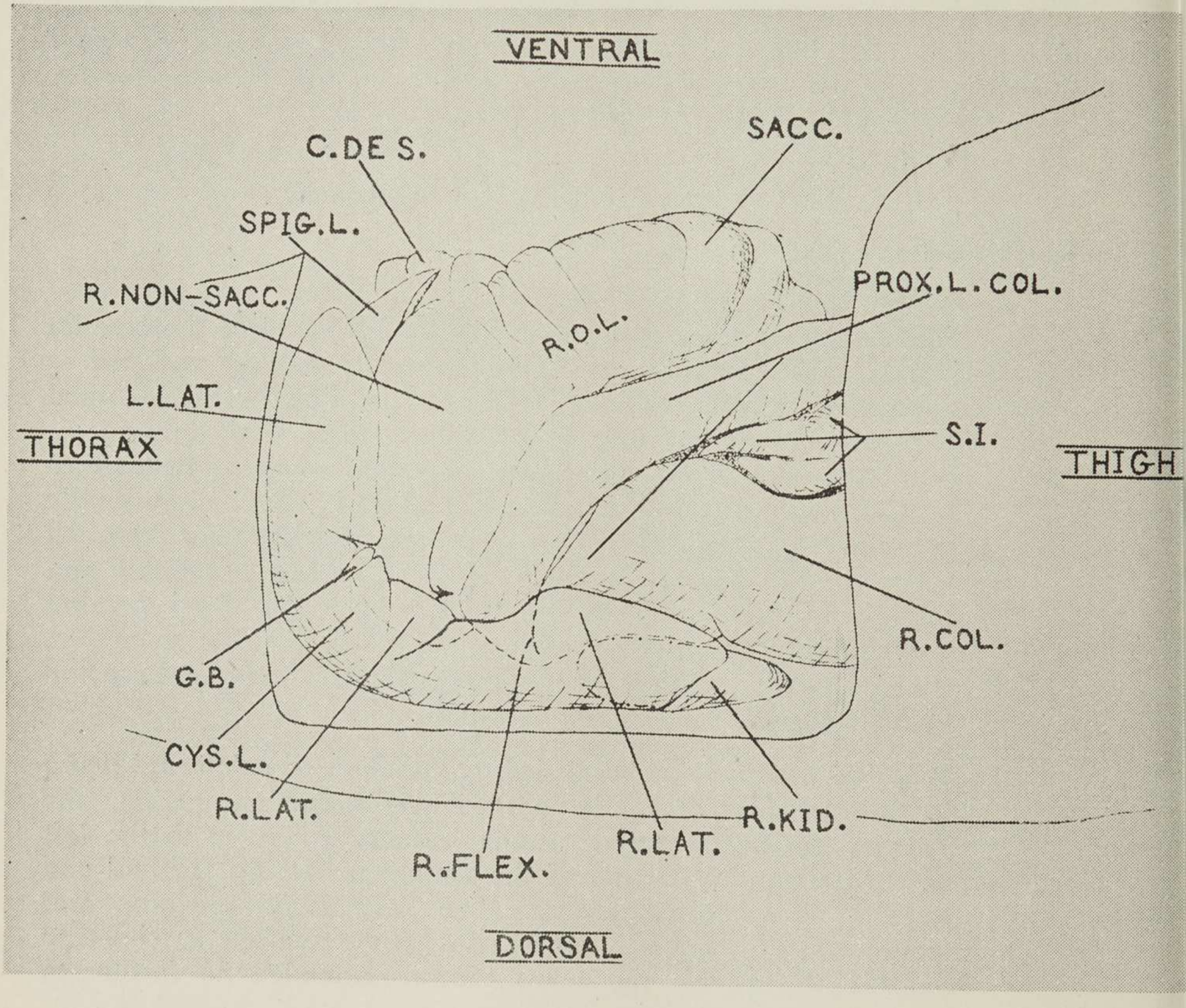
diac) portion of stomach; R.COL.—right (proximal) colon; R.FLEX.—right transpyloric or post-hypochondrial flexure of colon; R.NON-SACC.—right pyloric or non-sacculated portion of stomach; R.O.L.—right oblique limb of stomach; R.PR.SPL. —right (ventral) process of spleen; SACC.—sacculated part of right oblique limb of stomach; S.I.—small intestine; SPIG.L.—spigelian lobe of liver; TAEN.—a taenia of the stomach.

the left than the hypogastric region, whereas in one animal its distal tip lay in the left iliac region (text fig. 18a).

b. Shape and dimensions (text figs. 19–21, 23, 25).
Caecum of *Setonix* short, relatively wide, and rather blunt, maintaining a fairly constant calibre throughout its length. Length from 43 to 61 mm. and maximum circumference 60 to 85 mm.

The caecum in my specimens was not circular in section, but probably through pressure of adjacent viscera, was somewhat flattened. As the degree of flattening was about the same in all these specimens, comparisons of its width could be made (see also p. 103).

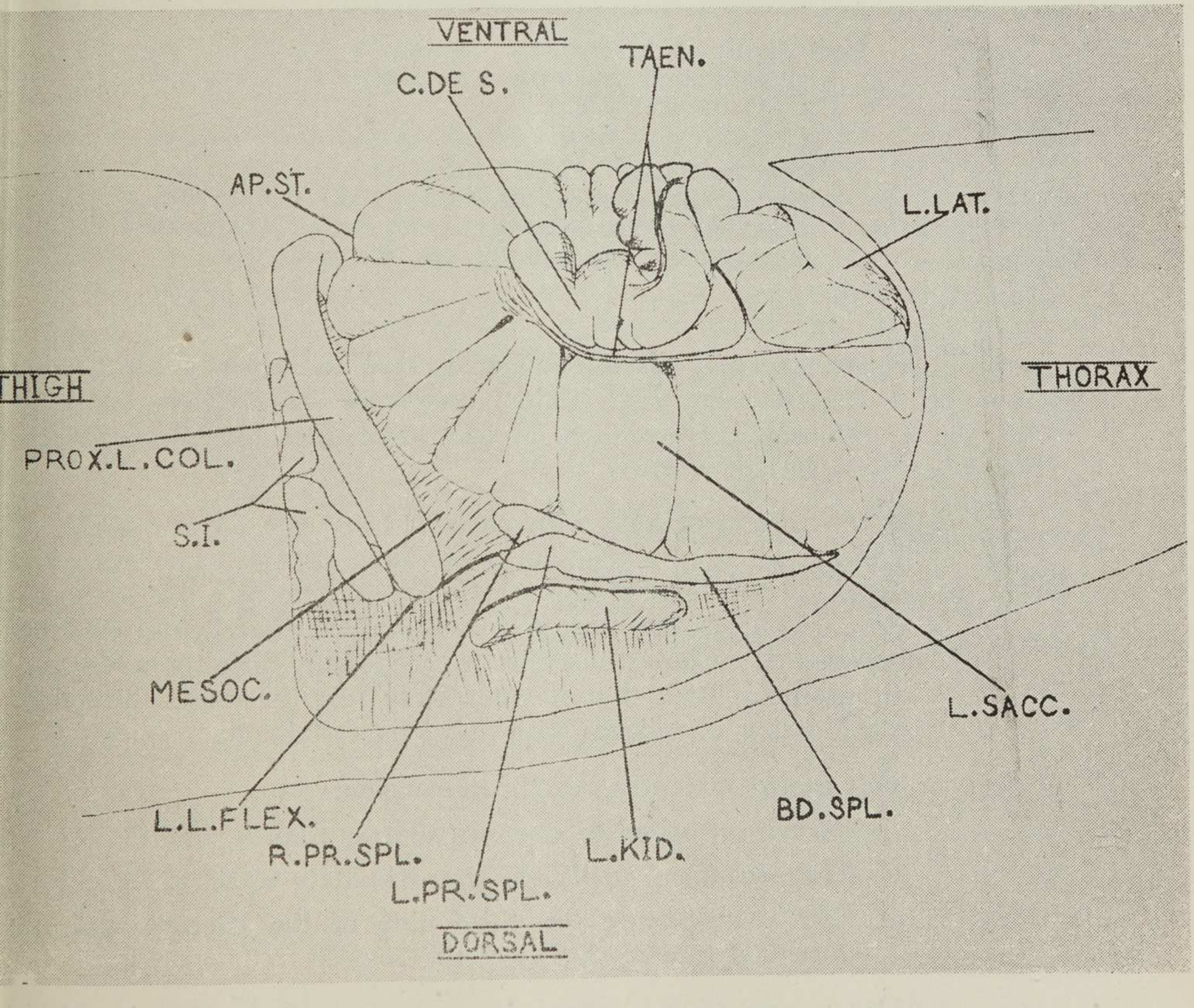


Text fig. 18b.—**S. brachyurus.** Right lateral view of anterior abdominal viscera *in situ.* (Not same specimen as is shown in text fig. 18a.) Note accommodation by lobes of liver of pyloric part of stomach, proximal part of colon and right kidney. Arrow indicates flexure of right pyloric part of stomach in right hypochondrium. Right transpyloric flexure of colon dotted in behind right lateral lobe of liver. ½ natural size.
G.B.—gall bladder; PROX.L.COL.—proximal part of left (distal) colon; R.LAT.—right lateral lobe of liver almost divided in two by fissure; R.KID.—right kidney. Other abbreviations, see text fig. 18a.

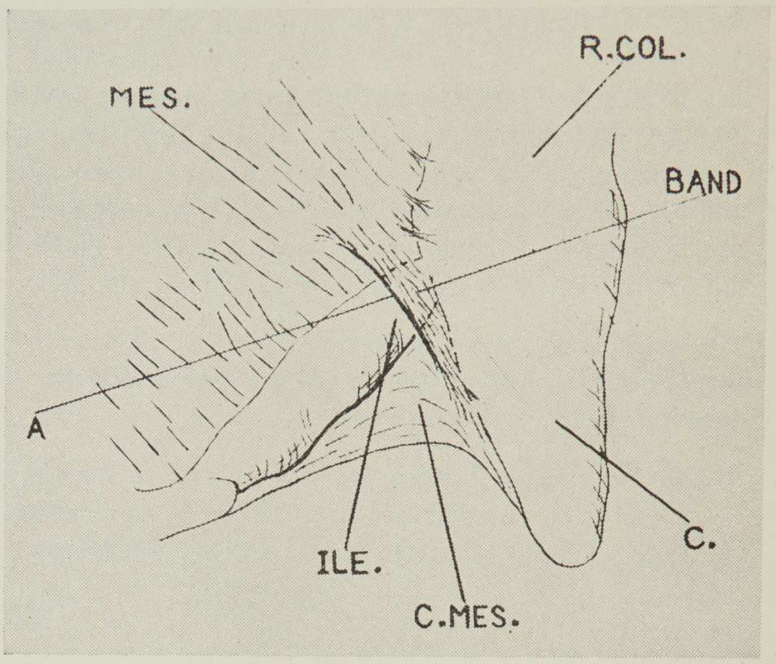
Maximum breadth about half its length. In two individuals the ratio of length to breadth of caecum was noticeably greater than 1.00 : 0.50; in the other four examined it was slightly less than 1.00 : 0.50. Probably the greater width of caecum in the two individuals was due to distention by food or to greater "flattening." Distension by food will also affect the shape, including the degree of tapering. For example, in specimen 2 the caecum, which was not greatly distended, narrowed noticeably towards its distal end. (Text fig. 19.)

c. Variations in shape (text fig. 22).
Specimen 6 showed some slight variations in the form of its caecum:—

i. Caecum curved along its length and could not be straightened without unnatural strain on the caecal mesentery. This curvature was not found in the other specimens.



Text fig. 18c.—**S. brachyurus.** Left lateral view of anterior abdominal viscera *in situ*. Same specimen as shown in text fig. 18b. ½ natural size. B.SPL.—body of spleen; L.KID.—left kidney; L.L.FLEX.—left lumbar flexure of left colon; MESOC—mesocolon of left colon. Other abbreviations, see text figs. 18a and b.



Text fig. 19.—**S. brachyurus.** Ileo-caecal region and associated peritoneal structures. Drawn from specimen 2. ½ natural size.

A—see p. 101; BAND.—band of mesentery crossing from mesentery of small intestine to caecal mesentery; C.MES.—caecal mesentery; ILE.—ileum; MES. mesentery of small intestine and right colon. Other abbreviations, see text figs. 18a, b and c.

ii. At proximal (basal) end of caecum there was a constriction (A, text fig. 22). Other abnormal constrictions of large intestine of specimen 6 are mentioned elsewhere in this paper (p. 102).

d. Mesenteries associated with caecum (text figs. 19 and 21). Position of caecum relative to proximal part of right colon and distal part of ileum is to a certain extent determined by a mesentery, which has the outline of an isosceles triangle and stretches between the adjacent margins of caecum and distal part of ileum. Its extent is such that it completely fills the angle formed by the junction of caecum with distal part of ileum.

This caecal mesentry has three margins:—

i. *Caecal*—attached to caecum, shorter than ii. or iii.

ii. *Ileal*—attached to ileum, approximately equal to iii.

iii. *Free*—constituting the third side of the triangle and not attached to any portion of the viscera.

Attachment of mesentery does not extend the full length of caecum but terminates 10 to 20 mm. from its blind end (cf. however, specimen 6 below). Free margin of mesentery concave. It is slightly thickened being therefore stronger than other parts of mesentery.

In specimen 6 (text fig. 22) the caecal mesentery extended to within 4 or 5 mm. of tip of caecum, instead of 10 to 20 mm. as in other specimens.

In every specimen a narrow band of mesentery crosses over the left of ileum near ileo-caecal junction; it connects mesentery of small intestine to caecal mesentery and is fused with both of them (text fig. 19). It has two margins—a free one, up to 20 mm. long (A, text fig. 19), and an attached one with adhesions to ileo-colic junction, to portions of mesentery of small intestine and to caecal mesentery. Except for these adhesions, the band of mesentery, as it crosses ileum, is quite free, and to an extent limited by this marginal adhesion to ileo-colic region, may be raised off the ileum. Width of this more mobile part of the band of mesentery (which is located about the middle of its length), may be up to 7 mm. Elsewhere along its length, the extent of the adhesion of the band to other structures, such as the mesentery of small intestine and the caecal mesentery, is increased and its mobility correspondingly decreased.

e. Conclusion on caecum.

Caecum and associated mesenteries of *S. brachyurus* do not differ markedly from the macropine condition described by Mackenzie (1918b, pp. 37-41) for other wallabies, though it is shorter and broader. Caecal mesentery of *Setonix* agrees with Mackenzie's description of that structure in wallabies, in that it does not extend to tip of caecum. However, it does not fall as far short of tip of caecum as that of the wallaby whose ileo-caecal region and associated mesentery is figured by Mackenzie (1918b, p. 38). Though no trace of the longitudinal bands described for the caecum of *Macropus major* (Mackenzie, 1918b, p. 39) could be seen on the outside of the caecum of *Setonix*, in specimen 1 (immature male) a longitudinal marking with transverse branches occurred on the inner surface directly underneath the attachment on the outside of the caecal mesentery. It was noticed after the mucosa had been scraped away. From this description it can be seen that the caecum and associated mesenteries of *Setonix* show some variation and may show slight differences from other wallabies.

2. *Evidence for "caecal pouch" in adults and pouch embryos.*

Mitchell notes that in *Macropus bennetti* (1905, p. 453 and fig. 8) and *Dendrolagus ursinus* (1916, pp. 197-8 and fig. 9), apart from the normal caecum, there is a "caecal pouch" also situated at the ileo-colic junction, whose position suggests that it is the remnant of the other member of originally paired caeca.

a. Examination of adults (text figs. 19-23, 25).

In adult the right (proximal) colon, which in five specimens shows no sign of constriction or sacculation, is, for greater part of its length, wider than caecum, this being particularly apparent at its proximal end in region of ileo-colic junction. Thus colon may be dilated at caeco-colic junction (text figs. 19, 20, 25). It was thought at first that the increased calibre of the proximal part of the right colon was evidence for Mitchell's "caecal pouch," but, after comparison of the conditions in *Setonix* with Mitchell's diagrams, this idea was abandoned. In both the species examined by Mitchell the caecal pouch is shown as a very definite structure, of quite appreciable length and boundaries, which, like the normal caecum, is directed along the ileum towards the proximal end of the small intestine. The dilation in *Setonix* is much less definite; it was completely absent from one of the specimens examined and its size varied in the other five. The variation is probably correlated with the amount of food contained in that part of the intestine.

In specimen 6, a male, a strikingly different condition was found (text fig. 22). Proximal part of colon had a total of six minor constrictions on its dorsal and ventral margins, and a seventh constriction at proximal end of caecum, near its junction with colon. Most prominent of these constrictions was on ventral margin of right colon, 30 mm. distad of ileo-colic junction (G. text fig. 22). It was 4 mm. deep, and, gradually losing its definition, extended from ventral margin of colon half way up its outer (right hand aspect). There was no evidence that it extended over the corresponding portion of the left hand side of right colon. Between it and ileo-colic junction there was a sacculus, which, if regarded as a poorly developed caecal pouch, was 4 mm. long (the depth of the constriction) and 27 mm. wide (the distance between the constrictions and the ileo-colic junction).

As can be seen from these dimensions and from text fig. 22, this structure, though striking in comparison with other specimens of *Setonix* which lack it, is not as prominent as the caecal pouch figured by Mitchell.

b. Examination of pouch embryos (for details of these see p. 61 and pp. 143-144).

Both specimens had the normal single macropine caecum. Right (proximal) colon was of uniform calibre, greater than that of ileum. As in adult, there was a slight dilation of right colon at ileo-colic junction but there was no sign of the sacculation seen in specimen 6. Thus there was no indication of a second caecal outgrowth in ileo-colic region of either pouch embryo.

c. Conclusion.

As I have been unable to examine the viscera of either *Dendrolagus ursinus* or *Macropus bennetti* for a first-hand comparison, a definite conclusion cannot be reached as to whether or not the sacculus on the ventro-lateral margin of the right colon of specimen 6 is a rudimentary caecal pouch. Though its dimensions and shape are not convincing in this respect, its position seems to correspond with that of the caecal pouch described by Mitchell in *D. ursinus* and *M. bennetti.*

It seems that this particular sacculus, whether it does or does not represent the second saecum of the original pair, is only exceptionally present in *Setonix,* as also are the other constrictions found on the right colon of specimen 6.

Examination of a larger number of specimens may or may not confirm this. Even if exceptional, the abnormality may be the persistance in an odd individual of an ancestral structure.

Whatever the significance of the condition of the right colon and caecum of specimen 6, it is peculiar and interesting. Rather than be evidence for a second caecum, as has been discussed here, it may represent a past or an incipient sacculation, by taeniae, of the colon.

3. *Comparative widths of ileum, caecum, and right colon in adults and pouch embryos.*

It is to be noted that, in the following brief investigation, comparisons are made between widths of the various parts of the intestine, not between circumferences. In all the animals I have examined the small intestine and right colon are flattened, so that the measurement of circumference, given in other sections of this paper, indicates better perhaps than the diameter the true calibre of sections of the intestine. Here, however, it was considered that: *Firstly,* in the adults examined, the flattening of the distal part of the ileum, caecum, and right colon was roughly the same so that comparisons of the widths of these three sections of the intestine, as indicative of relative calibres, could be fairly made. The same argument applied to the two pouch specimens in which the caecum, right colon, and distal part of the ileum were equally flattened. From the ratios of these measurements, any relative differences between pouch specimens and adults should be revealed. *Secondly,* the difficulties and possible errors involved in measurements of the circumferences of various parts of the intestine of small pouch specimens, would not justify attempting them in such a brief investigation.

a. Adults.
Maximum width of caecum about 2.5 times maximum width of distal part of ileum. Maximum width of right colon about 1.5 times maximum width of caecum.
Thus maximum width of right colon is about 3.7 times maximum width of distal part of ileum.

b. Pouch embryos.
Maximum width of caecum seems to be about equal to that of distal part of ileum in both specimens. In the older specimen, maximum width of right colon is about 1.5 times maximum width of caecum, and of ileum; in the younger, colon, caecum and ileum are of about equal calibre.

c. Conclusion.
From these facts it would appear that, as the animal gets older:—

i. Difference in calibre between ileum and caecum increases.

ii. Difference in calibre between ileum and right proximal colon increases.

It may be that the difference in calibre between caecum and right colon becomes marked at an earlier stage in the animal's life than i. above.

In most of the adults examined, the right colon and the caecum were distended with bulky vegetable matter, made up largely of complex polysaccharides undergoing the final stages of digestion and absorption. However, in specimen 1 (immature male) the right colon was contracted and empty (circumference 35 mm.), being of smaller calibre than the left (distal) colon (circumference 55 mm.) and not much larger in calibre than the distal part of the ileum. The caecum of this animal contained an appreciable quantity of matter, the passage of which into the right colon was probably prevented by the contraction of a caeco-colic sphincter. Presumably in this animal, prior to its capture, the matter originally within the right colon had moved on to the left colon to form faecal pellets, and additional supplies of vegetable matter had not reached the right colon from the small intestine or caecum: the right colon was therefore not distended.

The pouch specimens had a diet of milk and not of bulky vegetable matter: digestion of the milk would take place before it reached the large intestine. This food would yield a very small amount of indigestible or undigested matter in the hindgut. Though some faecal material would be provided possibly by dead intestinal flora and fauna (bacteria and protozoa), there would be no cause nor use for an expanded right colon or caecum. The latter, despite the complexity of the macropod stomach (cf. ruminants), probably plays a part in the digestion of the complex polysaccharides of the vegetation on which the adult feeds, and so in adults is voluminous.

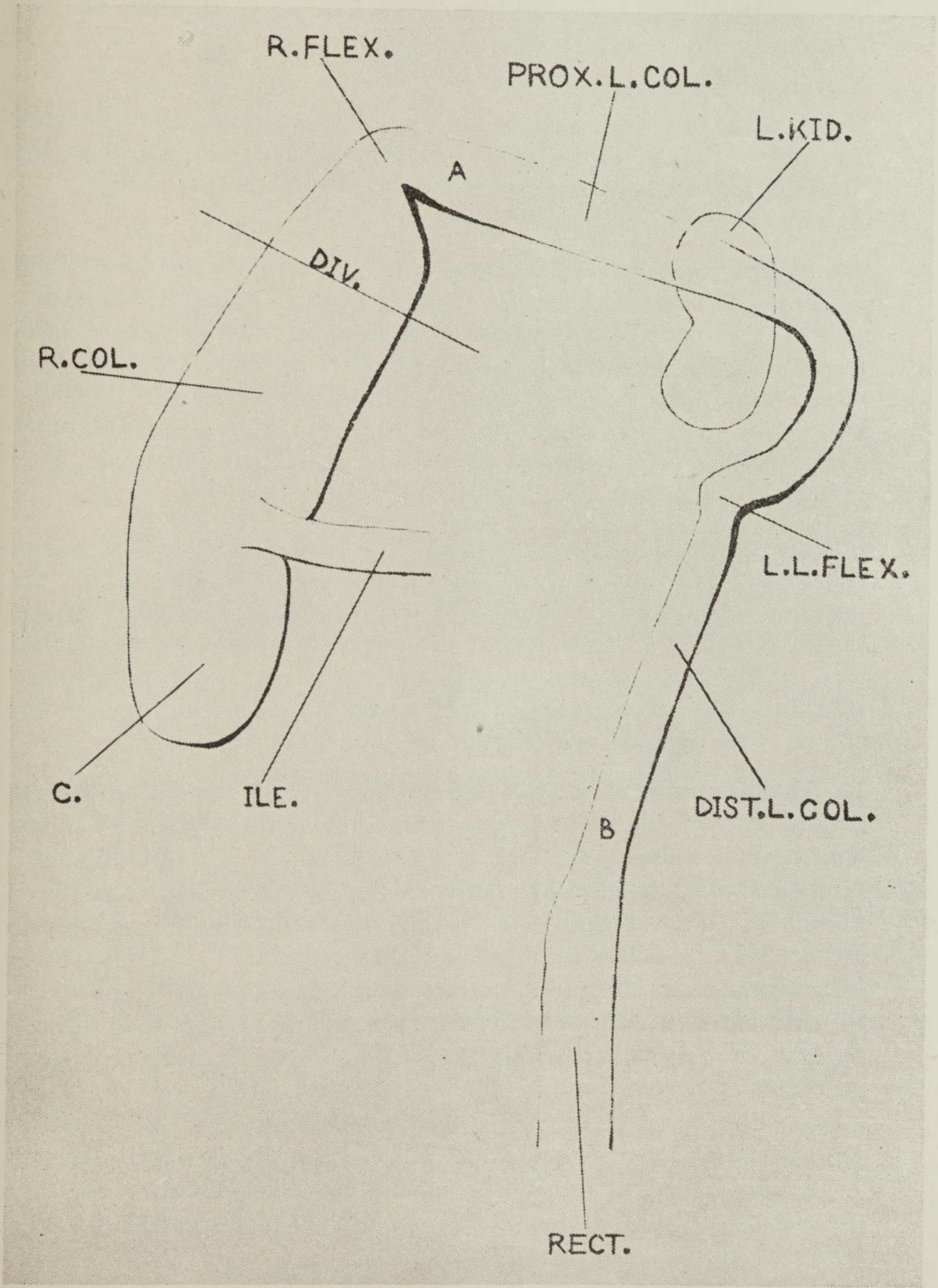
It is suggested, then, that in the adult, the calibre of the right colon and the caecum can probably vary considerably depending on the presence or absence of bulky vegetable matter. It may be that in an adult whose right colon and saecum are empty, the differences in calibre between these and the ileum might not be so apparent and the relative widths of these sections might approach more closely those in pouch specimens than do the results of my measurements. Experimental verification of the suggestion that differences in calibre between ileum, caecum, and right colon are the result of a change from a milk to a herbivorous diet, might be obtained by feeding a growing quokka on a milk diet for a longer period than the natural one: in this case differences of calibre like those mentioned above, might not be apparent. In the exceptional immature male specimen (see above) the empty right colon had walls which were much more muscular than those of the ileum. Hence it may be that, in the change from a milk to a vegetable diet, the essential change in the right colon is the development of more muscular wall, enabling considerable distension when the occasion demands.

C.—HIND-GUT.

1. *Introduction.*

a. Length.

Total length of hind-gut in *Setonix* is 440 to 520 mm. (cp. Beddard, 1908, p. 568). Calibre varies along its length, the



Text fig. 20.—**S. brachyurus.** Ventral view of large intestine to show its simple pattern. Left kidney shown to indicate relationship between it and left lumbar flexure of colon. All other viscera omitted. ½ natural size.

A to B—? Ansa coli sinsitra; DIST.L.COL.—distal part of left colon; RECT.—rectum. Other abbreviations, see text figs. 18, a, b and c.

maximum being in ileo-colic region. Distad there may be sudden variations in calibre due to accumulation or complete absence of faecal matter. Approximate circumferences, indicating the range in calibre for any one division of the hind-gut, are given in the descriptions of those divisions.

b. Pattern (text fig. 20).

Broadly speaking, the hind-gut of *Setonix* is ∩ shaped, the left arm being longer than right.

c. Divisions.

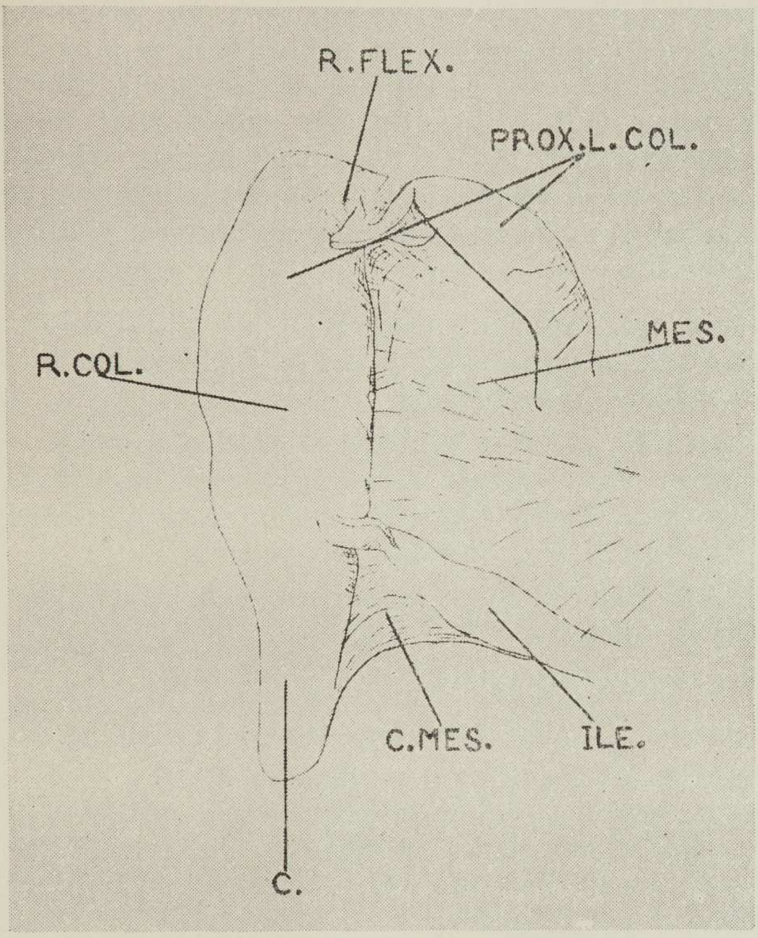
Hind-gut is divided into colon and terminal rectum. Rectum and urino-genital system joined to form a common chamber, the cloaca which opens to the exterior beneath the tail (see p. 91 of "Externals").

The colon (text figs. 18a, b and c, 20-23; 25-31) can be divided in right (proximal) and left (distal) parts. Mackenzie (1918b, p. 21) claims that this division is marked by the mesial fold, which is a sheet of peritoneum, to be described later, binding the colon to the pyloric region. Later, when dealing with the kangaroos and wallabies, he says that "The pyloric sphincter indicates the separation of the colon into two portions . . ." (1918b, p. 41).

For purposes of measurement of the various sections of colon, the pyloric constriction at distal end of sphincter, i.e. the junction of pylorus and duodenum, which, in *Setonix,* corresponds roughly with the point of closest adhesion by the mesial fold, of the colon to the pyloric regions, is regarded as the point marking the distal end of right, and the beginning of left colon (text figs. 20 and 23).

In *Setonix* there is a well-defined flexure of the colon in the caudal part of the right hypochondrium, at the right end of the transpyloric plane (text figs. 18a and b, 20, 21, 23, 25, 26); this might be taken as a flexure between the two sections of the colon. However, it is considered: *Firstly,* that the right transpyloric flexure of the colon is, relative to other viscera, more variable in position than the point of closest adhesion of the mesial fold to the pylorus at the pyloric constriction. *Secondly,* that the definition of this flexure is variable, being quite sharp in some specimens, but in one being more in the nature of a gentle curve. The point of closest adhesion of the mesial fold together with the associated pyloric constriction is in all cases well defined. Thus, this flexure is considered unsuitable as a boundary between the two sections of the colon. It is 25 to 55 mm. cephalad to the point of closest adhesion.

The well defined free cephalic margin of the mesial fold, seen only where the latter extends dorsad over the pylorus to become continuous with the lesser omentum of the stomach (text fig. 23), may provide a second suitable division of the colon into two parts. This margin does not vary in its relative position and, as will be discussed later, marks the point of continuity



Text fig. 21.—**S. brachyurus.** Ventral view of ileo-caecal region together with right colon and proximal part of left colon. ½ natural size.

Abbreviations—see text figs 18a, 18b, 18c and 19.

of the greater omentum (associated with the left colon) with the mesial fold (associated with the right colon). Though this continuity of greater omentum and mesial fold is not seen in all marsupials, in some, including *Setonix,* it may provide a suitable morphological division of the colon. This free cephalic margin is 25 to 35 mm. cephalad to the point of closest adhesion, and up to 25 mm. caudad to the right hypochondrial flexure of the colon.

Mackenzie (1918b, p. 43) recognises a proximal portion of the left colon, which, owing to the fact that it and its mesocolon have been included in the greater omentum, lies close to the greater curvature of the stomach. In *Setonix* the left colon has a well defined left lumbar flexure just ventral to the caudal end of the left kidney (text figs. 18c, 20, 26, 29). It so happens that, owing to the simplicity of the gut pattern in *Setonix,* nearly the whole of the left colon from its right hand junction with the right colon to this left lumbar flexure, is associated with the the greater omentum; on the right the greater omentum is attached to the colon itself and to the left, losing this attachment, it adheres to the mesocolon (text figs. 26) ; thus, apart from Mackenzie's division of the left colon into proximal and distal parts, by reference to the adhesion of the greater omentum to the colon or its mesocolon, this left lumbar flexure forms a convenient well defined boundary between the proximal and distal parts of the left colon. It is realised that this condition is peculiar to *Setonix* and any other form which may have a simple hind-gut.

There are, then, two flexures of left distal colon, one on the right side of transpyloric plane (right hypochondrial), the other in mid-left lumbar region.

Distal part of left colon extends caudad to pelvic cavity, where it passes into rectum (text fig. 29). Loss of the mesocolic support of hind-gut in pelvic region, separates colon, which has this support, from rectum, which lacks it.

The position of the colon *in situ* will be considered under its various divisions.

The rectum is considered on pp. 128-140.

2. *Right* (*proximal*) *colon* (text figs. 18a and b, 20-25).

a. Position *in situ* (text figs. 18a and b).

Right colon is quite straight throughout its course, showing no signs of sacculation or of ansa coli dextra. (For terminology see Beddard, 1908, pp. 593-594 and fig. 123; Mitchell, 1916, p. 187 and pp. 193-199).

The aberrant condition of proximal part of colon of specimen 6 has already been referred to (see pp. 99 and 102 and text fig. 22).

Right colon lies ventral to duodenum, but in the right dorsolateral part of abdomen, and extends through the right lumbar region from the trans-tubercular almost to the trans-pyloric plane.

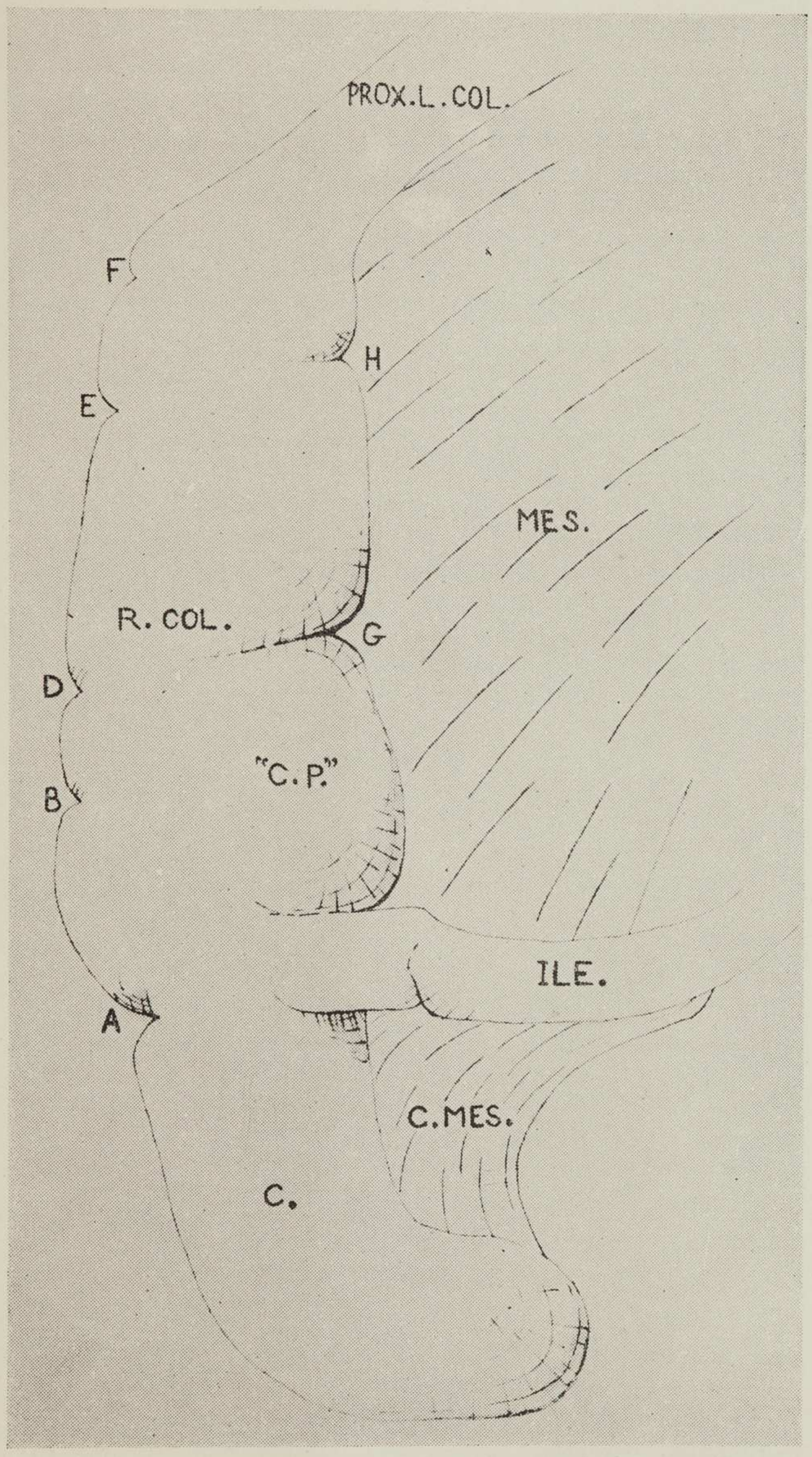
b. Dimensions.

Length of right colon, 35 to 50 mm. In adult right colon is not circular in section, but flattened laterally. It is greater in calibre than any other part of intestine, its circumference at proximal end (ileo-colic junction) being 80 to 100 mm. It narrows very slightly towards distal end, where the circumference is 70-90 m.m. In four specimens the maximum circumference was a few millimetres distad of ileo-colic junction; in two the maximum was nearer distal end. This variation may be partly due to variation in the distribution of the vegetable matter in this part of the hind-gut. Reference is again made to the immature male animal in which the right colon, empty of food, was narrow and contracted and more nearly uniform in bore throughout than in other specimens (see also p. 104).

c. Support.

Fixation of right colon within abdominal cavity is effected by:

i. The mesentery (text figs. 21 and 22) along portions

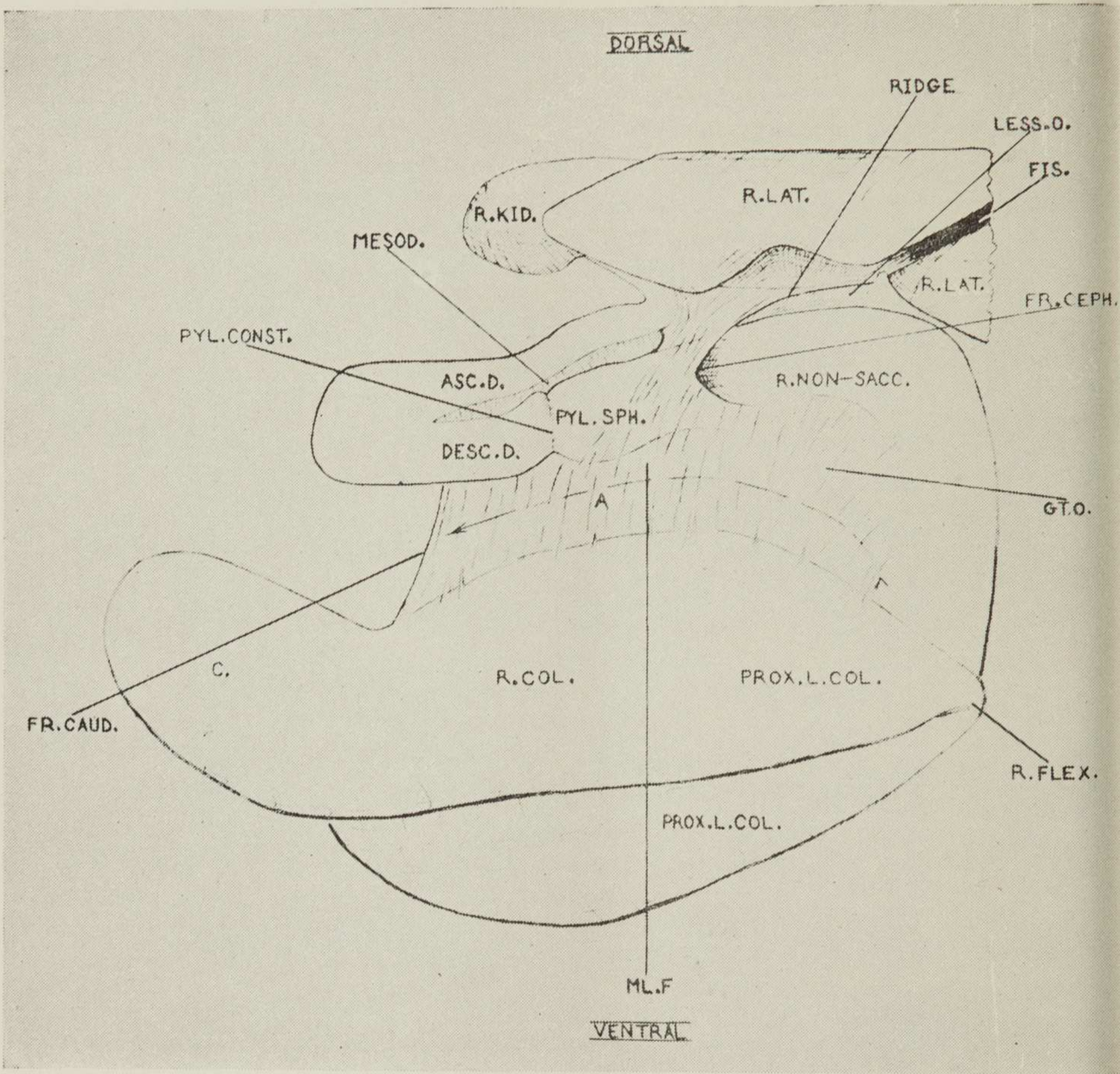


Text fig. 22.—**S. brachyurus.** Ventral view of ileo-caecal region, right, and proximal part of left colon of the abberant specimen 6. Natural size.

A—constriction at proximal (basal) end of caecum; B, D-H, constriction of proximal part of colon; C.P.—sacculus on proximal part of right colon corresponding in position to Mitchell's "caecal pouch." Other abbreviations—see text figs. 18a, 18b, 18c, and 19.

of the edge of which the right colon, and in another sector the small intestine, is suspended.

ii. The mesial fold (text figs. 23-25)—which is a sheet of peritoneum extending between distal two-thirds or more of right colon and proximal half to two-thirds of descending limb of duodenum, together with distal portion of pylorus (text fig. 23).



Text fig. 23.—**S. brachyurus.** Right lateral view of colico-duodenal and colico-pyloric regions with the associated peritoneal structures. The viscera have been displaced slightly ventrad. Arrow indicates right hand caudal prolongation of the lesser sac. 2/3 natural size. A—region of closest adhesion of colon to duodenum; ASC.D.—ascending limb of duodenum; DESC.D.—descending limb of duodenum; FIS—fissure dividing right lateral lobe of liver into two parts; FR.CAUD.—free cadual margin of mesial fold; FR. CEPH.—free cephalic margin of mesial fold; GT.O.—right hand end of greater omentum; LESS.O.—lesser omentum; MESOD—mesoduodenum; ML.F.—Meisal fold; PYL.CONST.—pyloric constriction (junction of pylorus and duodenum); PYL.SPH.—pyloric sphincter; RIDGE.—continuation of free cephalic margin of mesial fold to fissure dividing right lateral lobe of liver in two. Other abbreviations—see text figs. 18a and b.

(a) Margins—Mesial fold may be considered to have four margins:—

  (i) Colonic: attached to right colon. Length of attachment varies from individual to individual. It usually involves at least the distal two-thirds, even the whole of right colon.

  (ii) Duodenal-pyloric: attached to the descending limb of duodenum and to distal part of pylorus. Length of attachment varies from specimen to specimen, extending along proximal half to two-thirds of descending limb.

  Its attachment to pylorus is to its outer right hand side.

  Near the pyloric constriction (junction of pylorus and doudenum) the attachment (really a reflection of peritoneum from the gut) moves from outer side of this part of gut across ventral aspect of descending limb, and extends to inner angle of bend in duodenum (text fig. 24).

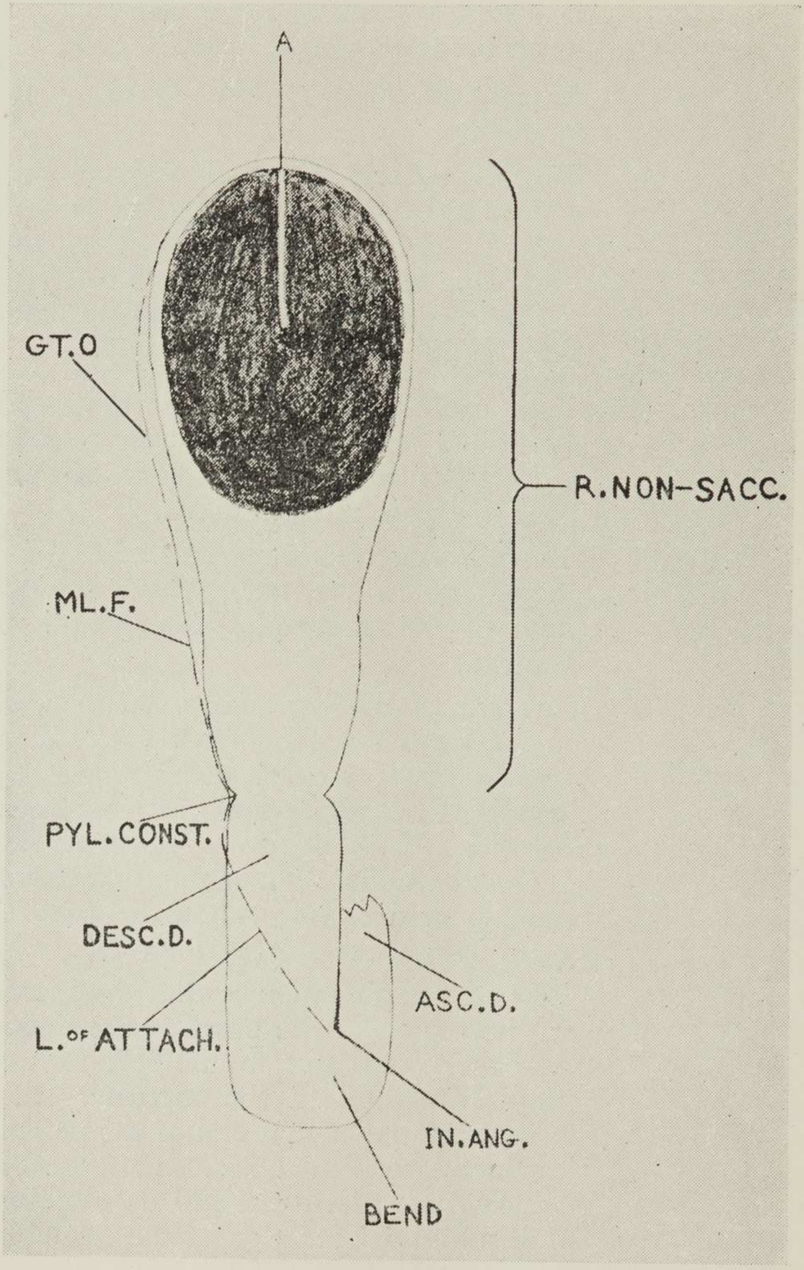
  (iii) Free caudal: which represents caudal limit of band and, when stretched, may be concave. Extends from inner angle of bend of duodenum to proximal part of right colon.

  There is a cavity between mesial fold on the right, mesentery on the left, pylorus and descending limb of the duodenum dorsad and right colon ventrad.

  Because of the continuity between mesial fold and greater omentum, this cavity is continuous with the lesser sac, of which it may be regarded as a right hand, caudal prolongation (arrow, text fig. 23). This prolongation of the lesser sac is closed caudad. The method of closure may be explained in one of two ways—which is correct I am not yet certain (text fig. 25).

  The first explanation is that the mesoduodenum in the region of the bend of the duodenum, extends ventrad and to the left to become continuous with both the mesentery of the right colon and the caudal end of the mesial fold. The distinct free caudal margin of the mesial fold, which runs dorso-ventrad (vertically), is produced by this extension of the mesoduodenum to meet the mesial fold at an acute angle. The intersection of these two layers of peritoneum produces a posteriorly-directed "apex" of this right hand caudal prolongation of the lesser sac, closing it posteriorly.

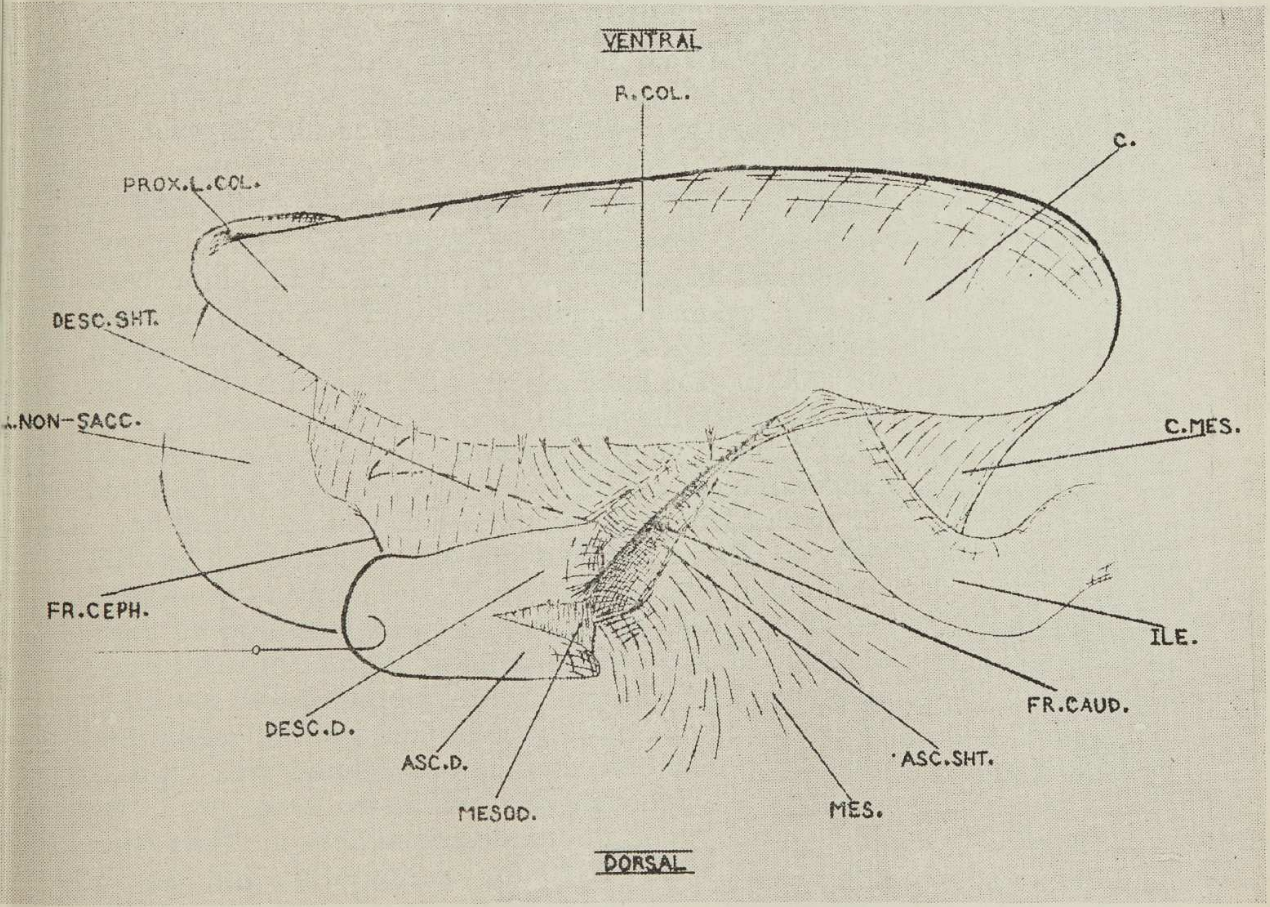
  The second explanation is that the mesial fold may be regarded as having two sheets, a long descending right hand one and a short ascending left hand one, closely related to each other and lying in a vertical (dorso-ventral) plane. That part of the mesial fold, already described as extending between colon ventrad and duodenum and pylorus dorsad, is regarded as the descending (right hand) sheet: this runs from the pyloric



Text fig. 24.—**S. brachyurus.** Semi diagrammatic ventral view of distal part of pyloric region of stomach and the duodenum, showing adhesion of mesial fold to duodenum and continuity between the cephalic end of this fold and right end of greater omentum. All other viscera omitted. Natural size. At A—rest of stomach removed by a horizontal section at its flexure in the right hypochondrium; BEND.—bend in duodenum; IN. ANG.—inner angle of bend in doudenum; L. OF ATTACH.—line of attachment of caudal part of mesial fold to descending doudenum. Other abbreviations —see text figs. 18a and 23.

region caudad as far as proximal end of right colon, where, co-incident with bending of duodenum to differentiate descending and ascending limbs, the mesial fold may be imagined to turn sharply to the left and run cephalad as the short ascending sheet. The ascending sheet becomes continuous at its cephalic end with the mesentery and the mesoduodenum. The caudal free margin of the mesial fold is formed where the descending sheet changes to the ascending one, thus closing the right hand prolongation of the lesser sac caudad (see also under *M. eugenii*).

(iv) Free cephalic—is seen where mesial fold extends dorsad over pylorus to become continuous with the lesser omentum. It has a definable length of 20 to 30 mm. and, along this length, is free from adhesions to other structures. A ridge, representing a continuation of this free margin, can



Text fig. 25.—**S. brachyurus.** Right lateral view of colico-duodenal and colico-pyloric region to show method of closure of right hand caudal prolongation of lesser sac (see p. 111). The doudenum has been folded forward over distal part of pyloric part of stomach, the "bend" having been pulled cephalad. 2/3 natural size.
ASC.SHT.—extension of mesoduodenum near bend of duodenum to mesentery and caudal end of mesial fold, or, alternatively, the short ascending left hand sheet of mesial fold, closing right hand caudal prolongation of lesser sac; DESC.SHT.mesial fold or "long descending right hand sheet." Other abbreviation—see text figs. 18a, 19 and 23.

be traced to fissure dividing right lateral lobe of liver in two (text fig. 23). The definition of the free cephalic margin of the band is lost after crossing pylorus to join lesser omentum dorsad, and as it approaches the colon ventrad.

Owing to the considerable transverse (right to left) extent of greater omentum, and to cephalo-caudal length of mesial fold, the latter, in the region of its free cephalic margin, becomes continuous with the greater omentum. This continuity explains, firstly, the loss of definition of the free cephalic margin of mesial fold as it approaches the right colon, having crossed the pylorus, and, secondly, the formation of a right caudal prolongation of the lesser sac. In an adult male *Trichosurus vulpecula,* the mesial fold and greater omentum were not so well developed and were not continuous. Thus the lesser sac was sealed off and had no right caudal prolongation. The continuity between the mesial fold and the right end of the greater omentum, and the mesial fold and the lesser omentum in *Setonix,* means that, in effect, the greater omentum is continuous with the lesser (see also Mackenzie, 1918b, 41).

(b) Width of mesial fold—free width of mesial fold at its caudal extremity, 30 to 40 mm. This is the maximum distance between right colon and duodenum in this region. Cephalad the band gradually narrows so that in region of pyloric constriction its free width is 20 to 25 mm. The "free" width has been emphasised; the band, is of course, continued over the duodenum and pyloric sphincter as part of visceral layer of peritoneum. It can only be freed from duodenum and sphincter by careful dissection. Where the mesial fold extends dorsad from greater omentum over pylorus to lesser omentum (cephalad to the pyloric sphincter), it loses adhesion to right (outer, lateral) wall of pylorus. Extent of this freeing of mesial fold varies a little from specimen to specimen. Associated with this dorsal prolongation of mesial fold to lesser omentum, is the well defined free cephalic margin of mesial fold seen where the latter crosses the pylorus. This has been described above. Thus there is a band which is 10 to 15 mm. wide and part of the mesial fold, extending from the greater to the lesser omentum.

d. Conclusion on right colon.

Thus in *Setonix* the right colon (particularly its distal portion) is close to the pylorus and duodenum. This is in accord with with previous general and particular descriptions. Flower (1872, pp. 291-294) and Mitchell (1916, p. 186 and Figs. 1A and B) have recognised that the beginning of the hind-gut and the duodenal region of mammals, tend to be close to each other. Klaatsch (1892, pp. 662-664) describes how the hind-gut with its "Flexura coli dextra." overlies the doudenum in *Halmaturus.* He says that in the region of the ligamentum cavoduodenale, connections are hinted between the duodenum and hindgut. He also claims that the colon approaches the duodenum in *Phalangista vulpina* (*Trichosurus vulpecula*). The views of Beddard 1908) and Mackenzie (1918b) on the subject of adhesions between the colon and duodenum, have been discussed on page 94 of this paper.

Mackenzie seems to recognise two separate adhesions in the colico-duodenal region—one which "passes across the thickened pyloric sphincter of the stomach from the right of the lesser to the right of the greater omentum" another which he describes thus, "We frequently see a peritoneal adhesion or band from the dextral margin of the right free colon to the descending duodenum, even as far as its lower third" (1918b, pp. 41 and 45). The inference is that there are two distinct bands of peritoneum, one extending between colon and pylorus, the other between colon and duodenum. The total extent of these two bands is the same as the single one described above for *Setonix.*

Any differentation of the single band in *Setonix* which might lead one to conclude that it arose as two separate structures, appears to be lacking in the specimens which I have examined. *Setonix* may therefore differ from the macropods examined by Mackenzie; his two (inferred) fold in the colico-duodenal region may be distinct in intrauterine and pouch embryos of *Setonix,* but if so, they lose their separate indentities in the adult.

The structure of the right colon in *Setonix* is, in a broad way, as Mackenzie (1918b, pp. 41-5) describes it for macropods generally, the only marked difference being that noted above.

3. *Left* (*distal*) *colon* (text figs. 18a and c; 20, 21; 26-29).
   a. As a whole.
      i. Position *in situ* (text figs. 18a and c; 20)—Generalised plan of left colon of *Setonix* is 7—shaped (text fig. 20). Beginning on right side of abdomen, where it is continuous with right colon, the left colon runs through the cephalic part of right lumbar region. At right side of transpyloric plane, near the bend within the right hypochondrium of lesser curvature of stomach, the left colon flexes sharply, running to the left across abdomen into the mid-left lumbar region (text figs. 18a and b). In left lumbar region, usually just ventrad to caudal end of left kidney, left colon flexes through about 90°, to run caudad into pelvic cavity, where it becomes continuous with rectum (text figs. 18c, 20, 26 and 29).
      ii. Dimensions. Total length of left colon, excluding rectum, 350 to 410 mm. As has been mentioned, its calibre varies, depending on the amount of faecal matter it contains. At

its proximal end, where it is continuous with right colon, the circumference is 70 to 90 mm. There is considerable reduction in calibre at flexure at right end of transpyloric plane, where the circumference may be only 10 to 20 mm. Distad of this flexure the maximum circumference may be 60 mm. and the minimum, measured on left colon as it approaches pelvis, and in a contracted condition, 20 mm.

iii. Support (text figs. 26-29). Whole of left colon is suspended on edge of mesocolon. In addition, proximal part of left colon, or its mesocolon, has additional support from the greater omentum, considerably reducing its mobility (text figs. 26-28). If left colon is considered to begin at the point of its closest adhesion to doudenum by means of mesial fold, then, since the mesial fold is continued cephalad beyond this point, the fold must be considered as attached to the first 25 to 35 mm. of the left colon

b. Proximal part of left colon (text figs. 18a, b and c; 20; 26-29).

i. *In situ* (text figs. 18a, b and c)—From its junction with right colon, ventral to pyloric sphincter, the proximal part of left colon extends through cephalic part of right lumbar region. At right end of transpyloric plane it flexes sharply to run more or less transversely across abdomen, following the greater curvature of the stomach, into the left lumbar region. Here there is the sharp caudal flexure differentiating the distal part of the left colon.

From its course in the abdominal cavity this part of the colon in *Setonix* may be called a "transverse colon." Proximal two-thirds of "transverse colon," lying close to right oblique limb of stomach, runs with a slight ventral component caudad and to the left (text fig. 18b). Close to apex of stomach, in caudal part of "umbilical" region (see Mackenzie 1918b, pp. 29-30), the "transverse colon" curves dorsad, running to the left lumbar flexure of the colon (text figs. 18a and c).

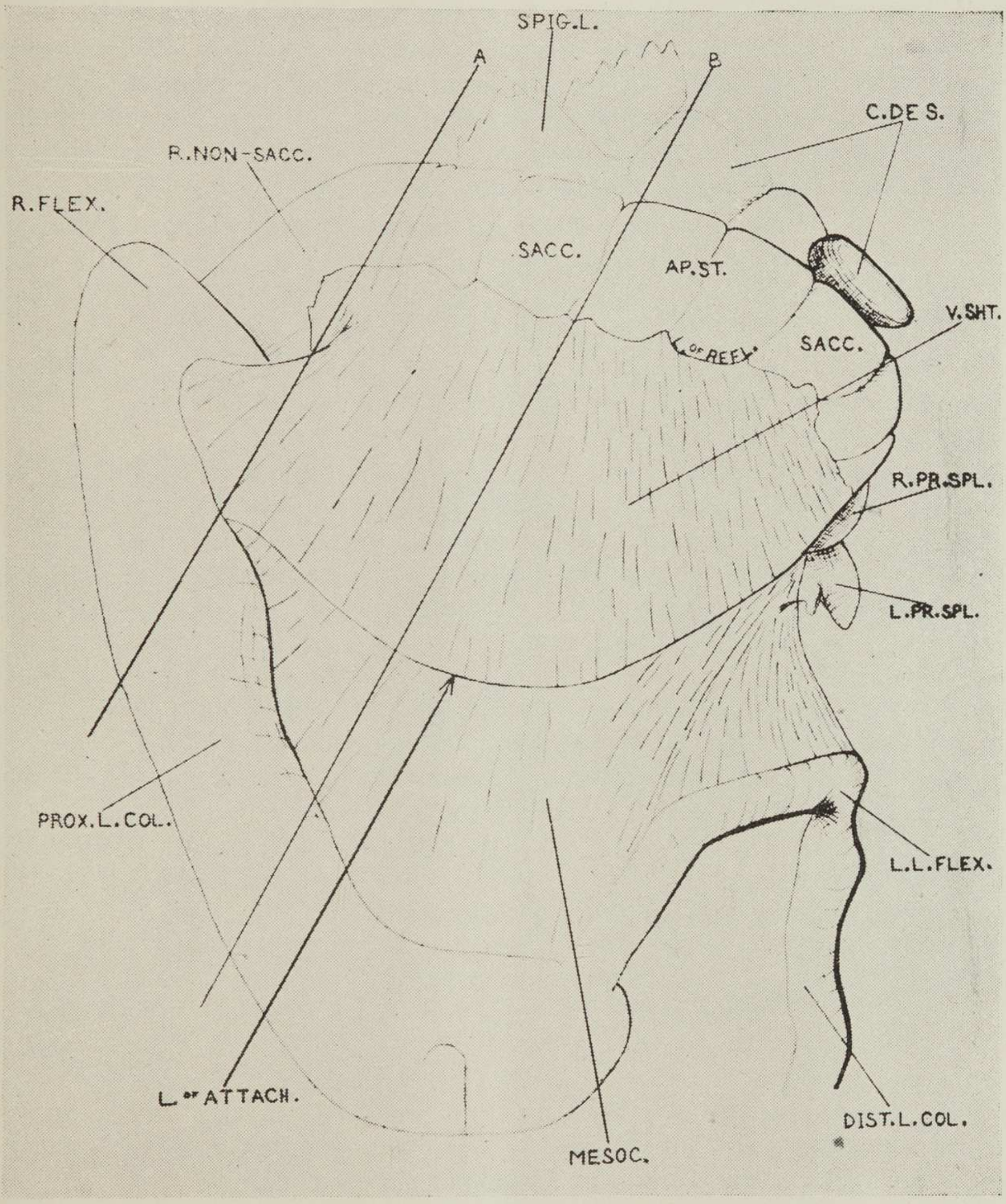
ii. Dimension—Proximal part of left colon is between 250 and 320 mm. long, 23 to 50 mm. of this being in cephalic part of the right lumbar region. At right hypochondrial flexure the calibre is greatly reduced so that the circumference of colon is between 10 and 20 mm. (cp. max. calibre, p. 115). At a point just proximal to left lumbar flexure of left colon, the circumference of the contracted and empty colon is about 25 mm.

In some animals faecal pellets were constricted off halfway along the "transverse colon" (text fig. 29).

iii. Support (text figs. 26-29). Fixation of proximal part of left colon is effected—

(a) By greater omentum (text fig. 26-28), the ventral sheet (descending or anterior sheet of human anatomy) of which is attached to right hand 60 to 80 mm. of "transverse" colon. Farther to the left, the greater omentum, no longer attached to colon itself, adheres to mesocolon of proximal part of left colon as far to the left as its left lumbar flexure (text figs 26).

The portion of proximal part of "transverse colon" to which greater omentum is attached, is closely bound to



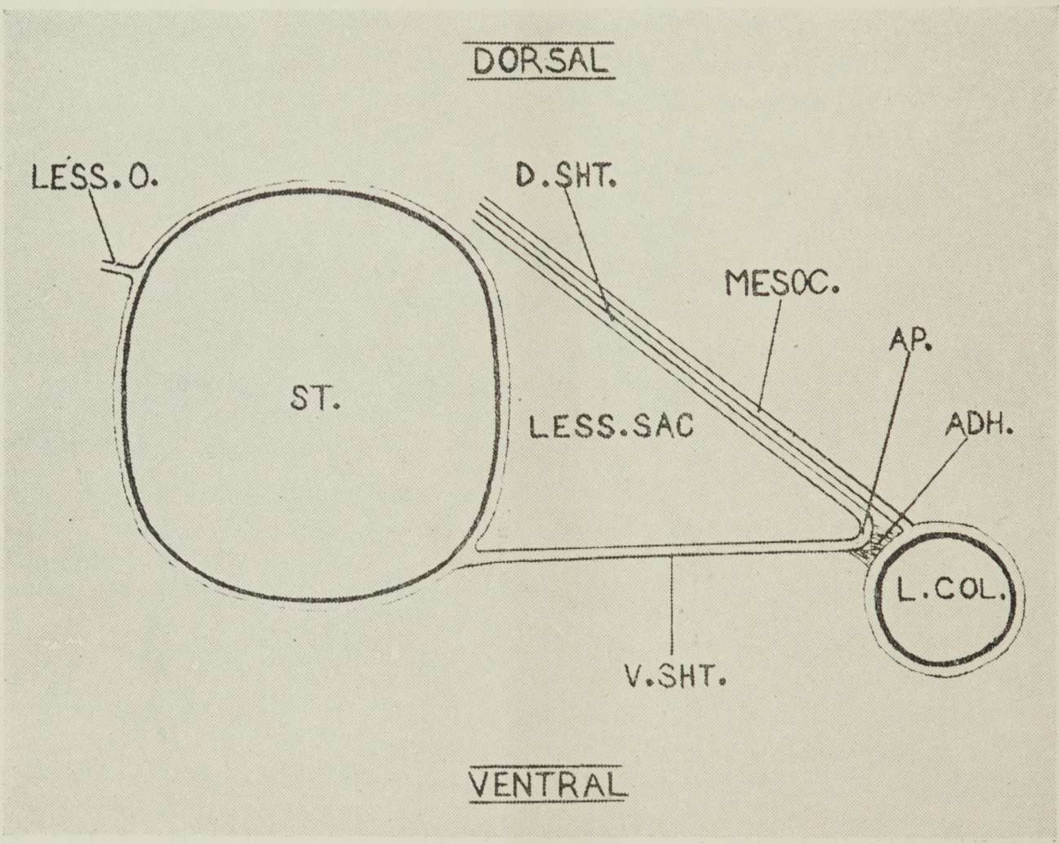
Text Fig. 26.—S. brachyurus. Ventral view of proximal part of left colon ("transverse colon") with associated greater omentum and mesocolon. Note considerable accumulation of faecal matter in proximal two-thirds of "transverse colon." In order to stretch and show clearly the mesocolon and greater omentum, the stomach has been pulled forward and the "transverse colon" back. 2/3 natural size.

A—approximate line of section for text fig. 27; B—approximate line of section for text fig. 28; L. OF ATTACH.—line of attachment (adhesion) of ventral sheet of greater omentum to mesocolon; L. OF REFL.—line of reflection of greater omentum (ventral sheet from greater curvature of stomach; V. SHT.—ventral (descending) sheet of greater omentum. Other abbreviations—see principally text fig. 18a; also text fig. 18b, 18c and 20.

distal half of right oblique limb of stomach. (This limb extends obliquely across abdomen from left lumbar region to right hypochondrium, and includes all the non-sacculated part of the stomach before its bend in the right hypochondrium, and a small portion—maximum of 35 mm.—of the distal part of the sacculated portion of the stomach).

In *Setonix* the inclusion of the proximal part of the transverse colon" in the lesser sac appears to be as follows—the caudad directed apex of the bag-like growth which forms the greater omentum, does not quite reach the left colon, but, falling a few millimetres short, sends out secondary connective tissue attachments to colon. Dorsal sheet of greater omentum (posterior or ascending sheet of human anatomy) is in close contact with mesocolon of "transverse colon," both where greater omentum is attached to colon itself and where it adheres to the mesocolon (text fig. 27).

The approximation of right hand portion of "trans-



Text fig. 27.—**S. brachyurus.** Diagrammatic transverse section through stomach and adjacent proximal part of left colon ("transverse colon"), showing relationship between greater omentum, mesocolon and "transverse colon." Line of section at A in text fig. 26. Figure also applies to first limb of left colon of **M. eugenii.** About natural size.

AP.—caudad directed apex of bag-like outgrowth formed by greater omentum; ADH.—connective tissue adhesion between apex of this bag and "transverse colon"; D.SHT.—dorsal (ascending) sheet of greater omentum; LESS.SAC.—lesser sac; ST.—stomach. Other abbreviations— see text figs. 18a and c, 23 and 26.

verse colon" to greater curvature of stomach, through the adhesion of the greater omentum, is closest on the right, where the greater omentum and the mesial fold are continuous (text fig. 26). At this point the distance between stomach and colon is 35 to 50 mm. (i.e. here the ventral sheet of the greater omentum is 35 to 50 mm. wide). The maximum displacement of "transverse colon" from greater curvature, without damage to the greater omentum or mesocolon, increases to the left, so that where the attachment of greater omentum to "transverse colon" is finally lost, at a point between 60 and 80 mm. along the latter, the displacement is between 55 and 65 mm. (i.e. at this point the width of the ventral sheet of the great omentum is between 55 and 65 mm.).

The separation, then, of the left colon from the greater curvature of the stomach is fairly gradual (see text fig. 26 and cf. *M. eugenii* in later note).

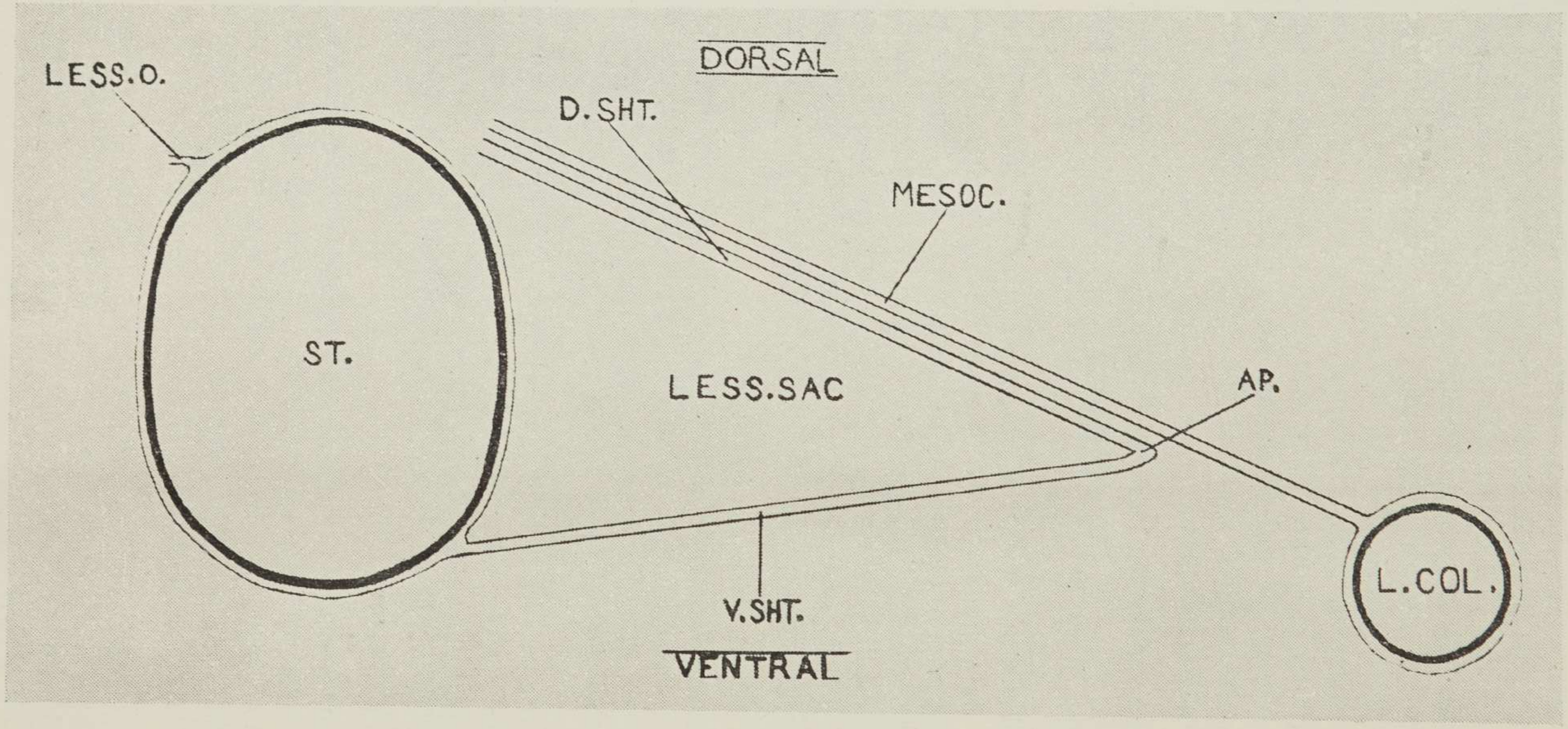
Maximum width of greater omentum (65 to 90 mm.). is at a point 10 to 30 mm. distad of apex of stomach along the latter's right oblique limb. Farther to the left, width of ventral sheet of greater omentum decreases, so that, at caudal end of body of spleen, which is supported from greater curvature of stomach by greater omentum, the width is between 15 and 25 mm.

Thus, on either side of the point of maxium width of the ventral sheet its width decreases to between 36 and 50 mm. on its extreme right, and 15 and 25 mm. on its extreme left (text fig. 26).

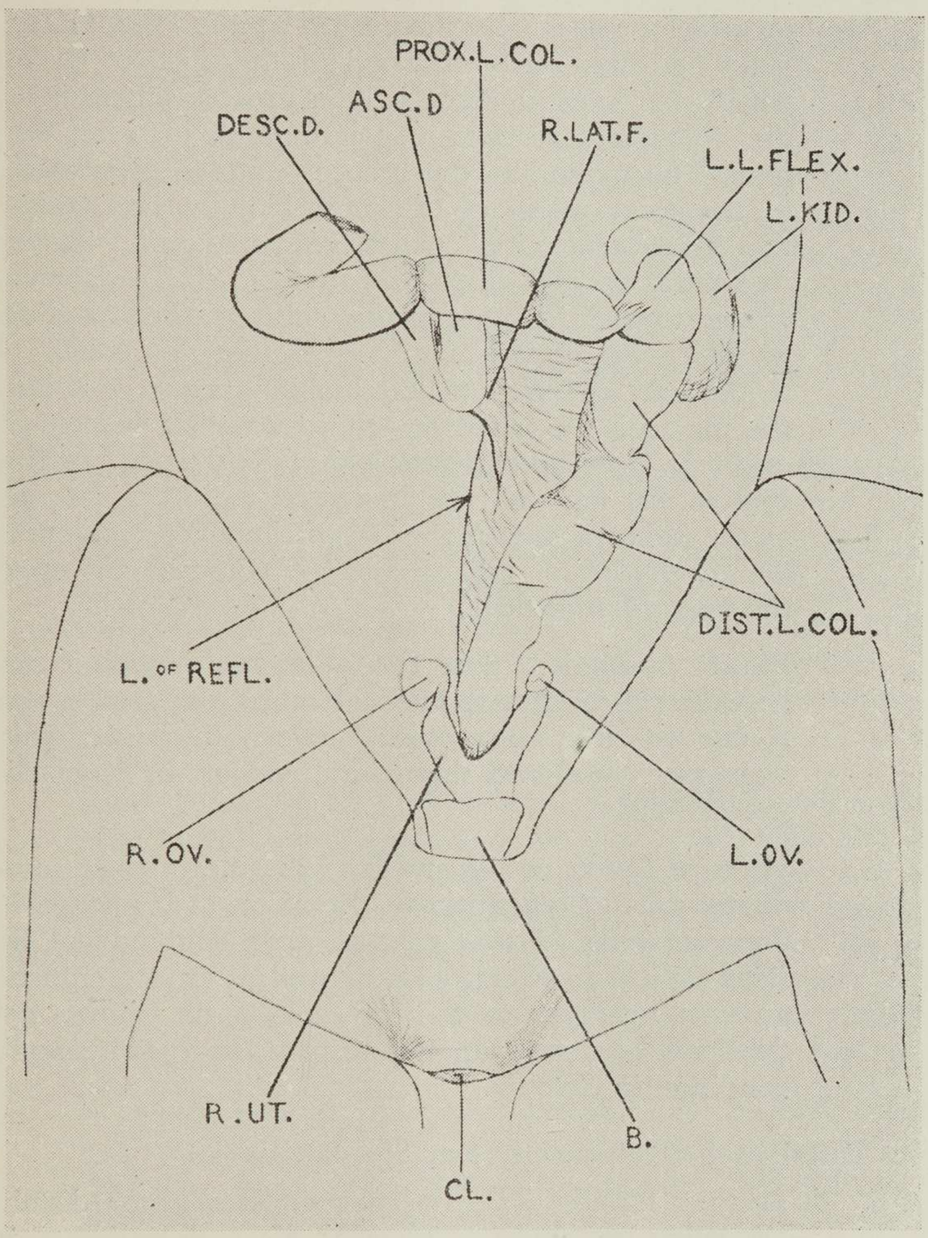
(b) By mesocolon (text figs. 26-28)—Mesocolon, supporting the whole of proximal part of left colon, is, broadly speaking, fan-shaped, the focus of the fan being in middle line of dorsal abdominal wall, level with cephalic end of left kidney.

Mesocolon of "transverse colon" reaches a maximum width of between 100 and 130 mm. at that part of the proximal portion of left colon near apex of stomach. At right and left ends of "transverse colon" the mesocolon is narrower (75 to 90 mm. wide).

iv. Conclusion on proximal part of left colon. The close relationship through the growth of the mesial fold, between right hand end of left colon and distal part of greater curvature of stomach (pylorus and duodenum), facilitates the extension and final adhesion of the greater omentum, arising from the greater curvature, to the proximal part of the left colon. However, the "influence" of the mesial fold's adhesion is gradually lost to the left. The greater omentum loses its adhesion to the left colon and is attached to the mesocolon



Text fig. 28.—**S. brachyurus.** Diagrammatic section through stomach and adjacent left colon ("transverse colon") showing relationship between greater omentum, mesocolon and "transverse colon." Apex of bag formed by outgrowth of greater omentum falls short of left colon, but adheres to mesocolon. Line of section at B in text fig. 26. Figure can apply to a very limited section in **M. eugenii**—after loss of direct adhesion of greater omentum to first limb of left colon (between **X** and **Y**, text fig. 30) (see p. 124). About natural size. Abbreviations—see text figs. 18a, 18c, 23, 26 and 27.



Text fig. 29.—**S. brachyurus.** Ventral view of proximal (transverse) and distal parts of left colon. Notice the formation of distinct faecal pellets in the "transverse" colon, as well as in the distal part of the left colon. ½ natural size.

L.O.V.—left ovary; L. OF REFL.—line of reflection of mesocolon of distal part of left colon from dorsal body wall; R.LAT.F.—right lateral (duodeno-mesocolic) fold; R.OV.—right ovary; R.UT.—right uterus. Other abbreviations—see text figs. 10, 18b and c, 20 and 23.

of the "transverse colon" as far to the left as the left lumbar flexure. The line of this attachment can be traced to the left for 80 to 140 mm., finally losing definition as it approaches the spleen. It diverges on the left from the line of attachment of the mesocolon to the "transverse colon" (text fig. 26). In the region of the apex of the stomach, where the ventral sheet of the greater omentum is wide, the divergence reaches a maximum of between 40 and 50 mm. This maximum divergence seems to be related in part to the great width of the mesocolon at this point, where the "transverse colon" will have a maximum mobility and maximum possible displacement from the greater curvature of the stomach. In spite of the width of the greater omentum at this point, it falls far short of the left colon. Farther to the left, in region of left lumbar flexure of colon, where the mesocolon is narrower, the divergence is less—30 to 45 mm. It is because of the loss of "influence" of the mesial fold to the left and the increased width of the mesocolon at the point of greatest width of the greater omentum, that the latter loses its adhesion to the colon and is attached to the mesocolon instead.

Flower recognises that the adhesion, in some mammals, between the transverse mesocolon and the greater omentum, is due to close connection between the right end of the transverse colon and the pyloric end of the stomach (1872, pp. 293-294).

Beddard (1908, p. 593 and fig. 122) indicates an attachment of the greater omentum to the colon in his Stage 11B, but does not refer in that case to a colico-duodenal ligament. However, in his Stage 111, as well as an attachment of the greater omentum to the left colon, he shows a colico-duodenal ligament. In this respect Stage 111 resembles the condition in *Setonix*.

c. Distal part of left colon (text figs. 20 and 29).

i. *In situ* (text fig. 29)—When seen *in situ*, the distal part of left colon gradually approaches the middle line as it passes caudad from left lumbar flexure to pelvis and rectum. It shows no signs of loops (ansae coli).

ii. Dimensions—Distal part of left colon is between 70 and 90 mm. in length, its circumference being between 20 and 50 mm., the variation being due to the amount of distension by faecal matter.

iii. Support (text fig. 29)—It is suspended on edge of mesocolon, which is reflected from middle line of dorsal abdominal wall. Length of reflection (attachment) is between 110 and 135 mm. Width of mesocolon at the left lumbar flexure between 25 and 35 mm., while halfway between left lumbar flexure and rectum it is between 5 and 16 mm. Rectum is without mesocolic support. Thus the mesocolon narrows caudad, the distal part of left colon having maximum mobility at its cephalic end near left lumbar flexure, the mobility decreasing as it travels through caudal part of abdominal cavity to rectum. Owing to bulk of surrounding coils of small intestine, the mesocolon of distal part of left colon does not hang in a vertical sheet from the mid-dorsal line, but is folded over to the left (text fig. 29): correspondingly colon is displaced to the left, the displacement being a maximum at its cephalic end, associated with its greater mobility in this region. As the mobility decreases caudad, so does the lateral displacement, until, within the greater (false) pelvis, the distal part of left colon hangs vertically from mid-dorsal line at the edge of the narrowed mesocolon. This change in attitude is due to decrease in the bulk of the surrounding viscera and to the narrowing of the mesocolon.

4. *Preliminary note on colon of **Macropus eugenii*** (text figs. 30 and 31).

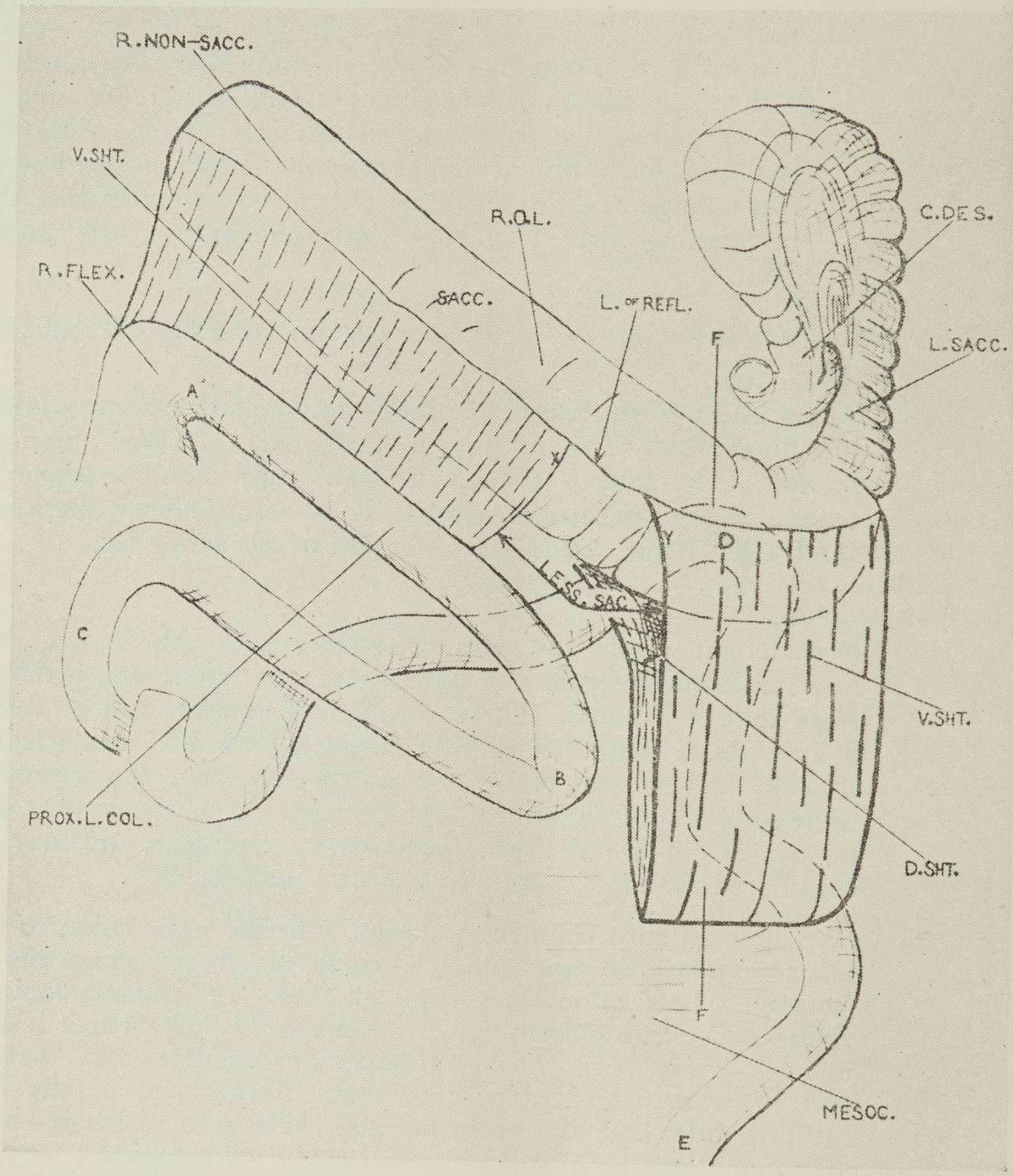
a. Mesial fold.

Mesial fold well developed and binds right colon closely to pylorus and duodenum. This binding appears to be closer than in *Setonix.* The fold is continuous with right hand extreme of ventral sheet of greater omentum. Thus, as in *Setonix,* there is a blind, right hand, caudal prolongation of the lesser sac.

b. Colon.

Right colon simple and without signs of ansa coli dextra. My brief examination does not show that, apart from size, it differs from that of *Setonix.* There is a flexure at right end of transpyloric plane. Total length of left colon is about 800 mm., greater than in *Setonix,* but this is not unexpected, since the animal is noticeably larger. However, the pattern of the gut is very different. It shows a well developed ansa coli sinistra and may be considered to have at least four limbs (text fig. 30).

First limb extends from the junction with the right colon to the left for about 130 mm. and is close to the greater curvature of stomach. Left colon then flexes on itself and extends back to right end of transpyloric plane as the *second* limb, which is also about 130 mm. long. This limb has minor undulations. At right end of transpyloric plane left colon flexes back to the left rather gently, and thus is formed the *third* limb which is about 400 mm. long and, indirectly, extends across cephalic part of abdominal cavity to the left lumbar region, dorsal to the first 260 mm. of the left colon. It has several fairly well defined undulations along its length. In left lumbar region, left colon turns to run caudad for about 150 mm. as the *fourth* limb of left colon, becoming continuous with rectum on reaching the pelvic cavity. Its course is fairly straight, there being one incomplete loop along its length. Whole of left colon in *M. eugenii,* as in *Setonix,* is suspended from the edge of mesocolon. First limb of left colon is the only section to which the greater omentum is attached (text fig. 30). It is this attachment, and consequent immobility of this part of colon, which differentiates it so clearly from the rest of left colon. It lies closer to greater curvature of stomach than does the corresponding part of the intestine in *Setonix*—the distance between the two parts in *M. eugenii* is not more than 25 mm. Loss of attachment of greater omentum to first limb corresponds approximately to the flexure between the first and second limbs. The greater omentum had been damaged just to the left of the point where it loses attach-



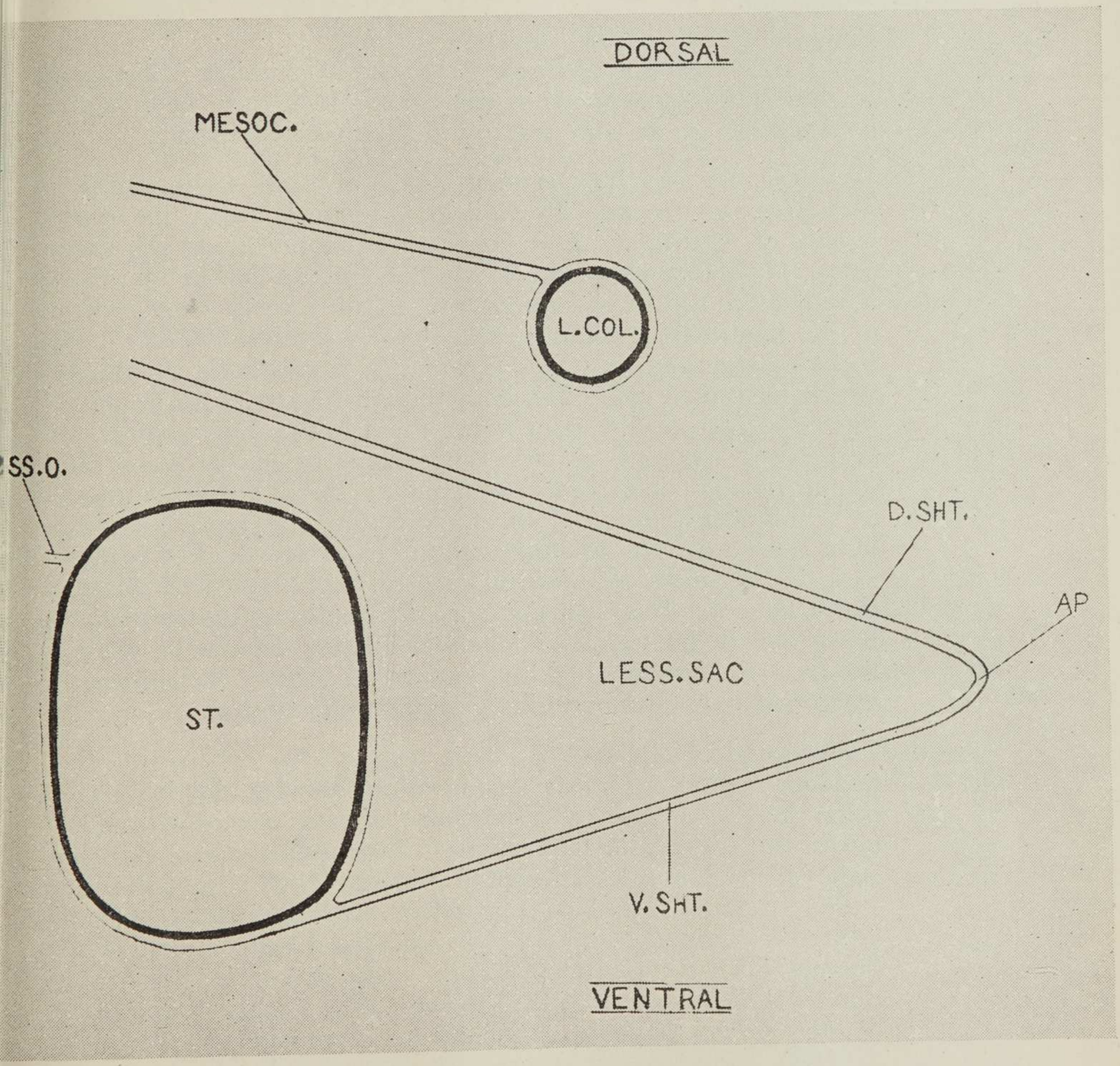
Text fig. 30.—**M. eugenii.** Ventral view of stomach and left colon with associated greater omentum. The left hand free portion of greater omentum has been emphasised. The mesocolon of fourth limb of left colon is shown. About ½ natural size.

A-B—first limb of left colon (=Mackenzie's proximal part of left colon); B-C—second limb of left colon; C-D—third limb of left colon; C.DE S.—bifid cul-de-sac of cardiac extremity of stomach; D-E—fourth limb of left colon. At D—? homologue of left lumbar flexure of left colon of **Setonix;** F—approximate line of section for text fig. 31. Between X and Y—greater omentum damaged. Other abbreviations—see text figs. 18a, b and c, 26 and 27.

ment to colon, but it seems that separation of greater omentum and colon is quite abrupt. Greater omentum appeared to be attached to mesocolon for a short distance on the left of its loss of attachment to colon. It then loses all connection with colon and mesocolon (text figs. 30 and 31). First limb of left colon, being included in the greater omentum and lying close to greater curvature of stomach, is the proximal part of the left colon (Mackenzie 1918b, p. 43); the rest of the left colon, supported in the abdomen simply by mesocolon, is more mobile than first limb and is not close to greater curvature of stomach.

c. Greater omentum (text figs. 30 and 31).

On the right, the greater omentum is continuous with the mesial



Text fig. 31.—**M. eugenii.** Diagrammatic transverse section of stomach and left colon (third limb) showing relationship between greater omentum, mesocolon and left colon. Line of section at F in text fig. 30. Greater omentum in this region does not adhere to left colon or any part of mesocolon, which is relatively narrower than that of the corresponding region in **Setonix.** Natural size. Abbreviations—see text figs. 18a and c, 23, 26 and 27.

fold. It is also attached to a portion of left colon (first limb) and to a small section of mesocolon. Dorsal (ascending) sheet of this part of greater omentum is closely applied to mesocolon supporting the first limb of left colon. However its left hand half, at least, is completely free of attachments to left colon or to mesocolon, as it descends from stomach or ascends to dorsal abdominal wall. It hangs from the stomach in the form of a bag, the blind end of which points cuadad.

5. *Conclusion on pattern of Colon of* ***Setonix.***

There is some difference of opinion as to the existence of ansae coli and the colico-duodenal ligament in marsupials.

a. Ansae coli.

Beddard (1908 p. 575) says:—

> "As a rule, with but few exceptions, the Marsupials possess none of those permanent loops of the colon which have been termed by Tullberg 'ansae coli,' and by Klaatsch 'flexurae coli.' "

However, he says he has seen signs of these colic loops in *Didelphys virginiana, Trichosurus vulpecula,* and in various species of *Macropus,* these genera presumably being the exceptions. His doubt about the existence of ansae coli in marsupials is indicated also in his description of the various basic patterns of the mammalian colon (1908, pp. 591-6; figs. 120-123). He includes *Macropus* in stages IIA and B, but excludes it from III, which has ansae coli. Mitchell, though he shows no ansae coli in the polyprotodonts, does figure them in the diprotodonts. He says, when speaking of wavy expansions or minor loops distal to the pendant loop in diprotodonts: "These are all supported by a simple expansion of the mesorectum and represent gradations from a merely expanded rectum to what would be regarded as a definite *ansa coli sinistra.*" (1916, p. 119). Thus Mitchell in his figures and text, is far more definite as to the existence of ansae coli in marsupials, than is Beddard. Mitchell's observations on the existence of a pronounced ansa coli sinistra in macropods, are corroborated by mine on *M. eugenii.*

b. Colico-duodenal ligament.

Beddard mentions secondary connections between doudenum and colon in *Trichosurus,* which I have seen in an adult male *T. vulpecula,* and says that marsupials show indications of this third stage of evolution of intestinal pattern (1908, pp. 593-6; fig. 123). Stages IIA and B (pp. 592-3) including *Macropus* and other marsupials, lack the colico-duodenal adhesion shown in Stage III. If the mesial fold is the same structure as the colico-duodenal ligament, it seems strange that Beddard should not be more emphatic about its occurrence in marsupials. Mackenzie (1918b) has seen the structure in Macropods, the Koala and Wombat, and I believe I have found it strongly developed in *M. eugenii* and *Setonix.*

It is apparent from comparison of my illustrations with those of the colon of macropods given by Mitchell (1905, pp. 451-452, figs. 7 and 8; 1916, p. 198), and from my observations on the

colon of *M. eugenii,* that its pattern in *Setonix* is simple.
In the macropods, whose intestines are figured by Mitchell, and in *S. brachyurus* and *M. eugenii,* the right colon is quite straight and without any signs of ansa coli dextra.

It is the left distal colon of macropods that becomes complicated by minor loops, and so the simplicity of *Setonix* lies in its left colon. Comparison with the left colon of *M. eugenii,* which has a well developed ansa coli sinistra, accentuates the simplicity of the pattern in *Setonix.* The left colon of *Setonix,* with its two flexures (right and left) and two *major* limbs (a transverse proximal and a caudad directed distal one) (text fig. 20), may represent a simple ansa coli sinistra.

In *Setonix* the proximal part of the left colon extends transversely across the abdomen from right to left. In *M. eugenii* the proximal part of the left colon (in Mackenzie's sense) is relatively shorter and extends only part of the way across the abdomen; there is a flexure in the left lumbar region differentiating the third from the fourth limb of the left colon (see text fig. 30 and p. 123).

However the left lumbar flexure of *Setonix* is more striking than that of *M. eugenii,* which has other undulations and loops on the left colon obscuring it (cf. *Setonix*).

It is not clear to me whether the left lumbar flexure of the colon in *M. eugenii* is the same as that in *Setonix;* i.e. whether the part of the left colon in *M. eugenii* which has minor loops and extends indirectly from the right end of the transpyloric plane transversely across the abdomen to the left lumbar region, is homologous with the "transverse colon" of *Setonix.*

Associated with simplicity of gut pattern of *Setonix* is the extensive attachment of the greater omentum to either left colon or its mesocolon. This relationship may extend for almost the full width of the cephalic part of the abdomen, from the right proximal end of the left lumbar flexure.

In *M. eugenii* there is a relationship between the lengthening of the colon (the development of an ansa coli sinistra) and the relatively less extensive attachment of the greater omentum to the left colon or its mesocolon. In this animal the association does not extend the full width of the abdomen, but is confined to the right hand half (see pp. 123 and 124).

Investigation has shown that in *Setonix* and *M. eugenii* the greater omentum is attached to portions of the left colon and the mesocolon, and that each has a well developed mesial fold (colico-duodenal ligament). A ligamentum cavoduodenale (right lateral fold) is also developed in *Setonix* (text fig. 29) and *M. eugenii. M. eugenii* has an ansa coli sinistra, which *Setonix* may possess in a simplified form. Neither have an ansa coli dextra.

Beddard (1908, p. 594) says that there are ". . . simpler forms and more complexly convoluted colons" in Stage III. As both the above forms have points in common with Stage III, they might be classified in that group as the "simpler forms" noted by Beddard. The colon of each certainly seems more complex than Stage IIB and if not strictly Stage III, is half way between it and IIB.

6. *The rectum and its peritoneal relations.*

I could find no account of the peritoneal relations of the pelvic viscera of marsupials in available literature. The identification of structures mentioned in my descriptions has been made by reference to Cunningham (1937) and Gray (1916). For details of the male urogenital system in marsupials, I have consulted Mackenzie (1919), and for the female system—Pearson (1944, 1945, 1946) and Mackenzie (1919).

Three pouches or cavities (recto-vesical, recto-uterine and utero-vesical) and their related folds of peritoneum, are described in this section. In ventral dissection of an animal these were collapsed and so at first did not appear as obvious as is suggested by the following description. Details of their size and shape given here are maximum values, obtained by stretching, without damage, the peritoneal folds, thus restoring them and the pouches to what was probably their maxium living extent.

a. What is the rectum?

From Cunningham's introductory remarks on the human rectum (1937, p. 617), from his discussion on its peritoneal relations (p. 620) and from Gray's remarks on the mesocolon of the sigmoid colon (1916, p. 1103), it is apparent that the rectum is part of the hind-gut which lacks a supporting mesentery mesocolon.

Mitchell (1916) on occasion uses "rectum" to cover that part of the gut distad to the end of the pendant loop (end of right proximal colon)..

In this paper the point where the mesocolon terminates is taken as the cephalic end of rectum. Here the process is begun which leads ultimately to the ventral wall of the rectum alone being covered with peritoneum. The caudal end of rectum is marked by its junction with urogenital system to form cloaca.

b. Course of rectum.

It runs straight through pelvic cavity. Length in five specimens was 60 to 85 mm. Circumference ranges from 30 to 60 mm. the variation being dependent on the quantity of faecal matter.

c. Support of rectum within pelvic cavity.

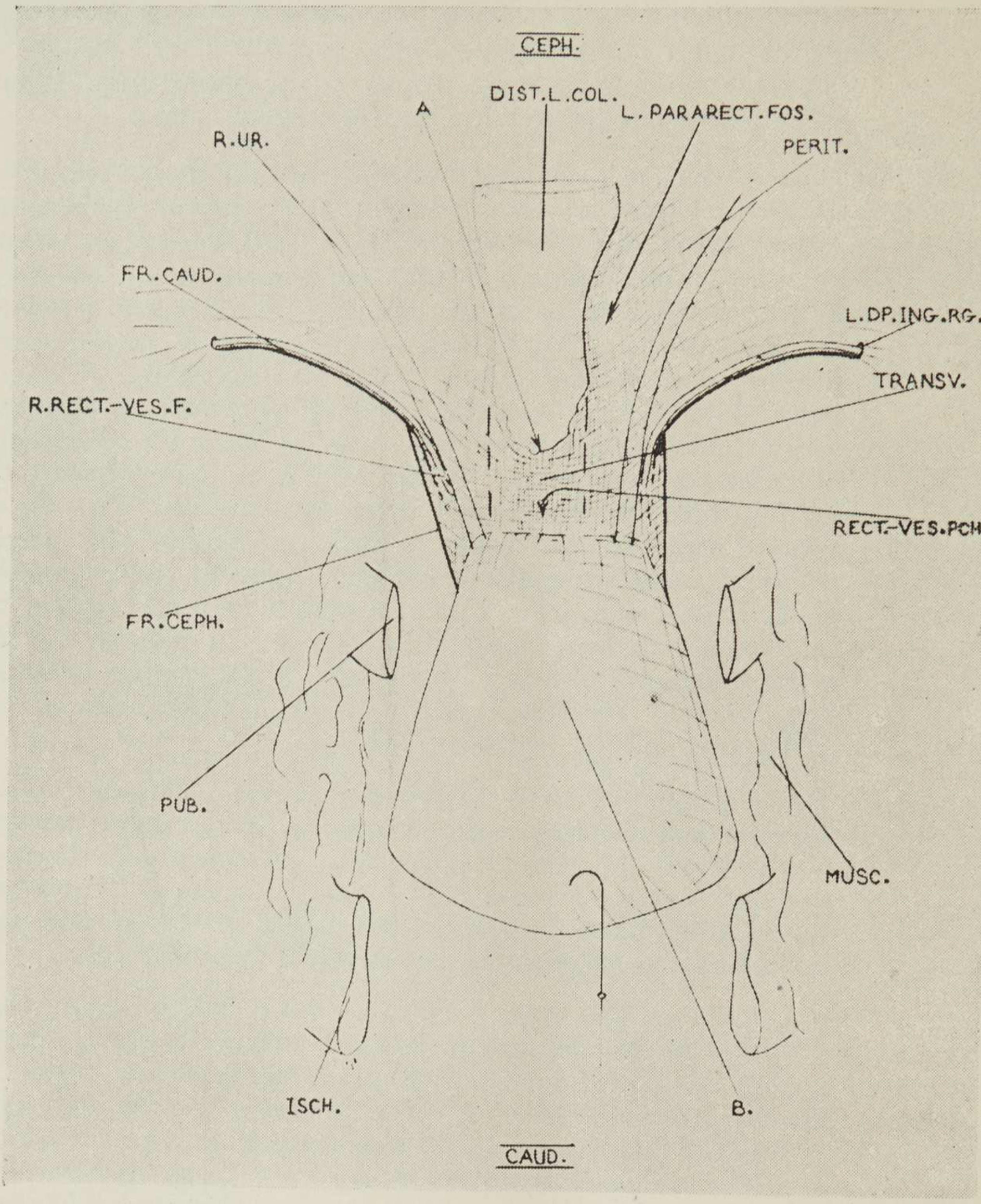
i. Loss of mesocolon in both sexes.—It has been indicated that the mesocolon supporting distal part of left colon within the greater (false) pelvis, narrows as colon approaches cavity of lesser (true) pelvis, i.e. as it approaches the cavity of lesser pelvis, the mobility of distal part of left colon is reduced (text fig. 29). In the region of inlet of lesser pelvic cavity and through the space of from 5 to 15 mm., the mesocolic support of left colon is lost. Mesocolon becomes detached from the dorsal, and later from the lateral, walls of rectum which finally, in the cephalic part of the lesser pelvic cavity, has peritoneum applied merely to its ventral wall. Thus, as Cunningham (1937, p. 620) has pointed out in describing the human rectum, because only its ventral wall has peritoneum applied to it, it lies dorsal to the peritoneum. Thus rectum does not project far into peritoneal cavity.

ii. Introduction on peritoneal adhesions within the pelvis.—For the greater part of the abdomen, the various components of the viscera, though in close contact, and despite peritoneal adhesions and supports, retain some measure of mobility. However the volume of the body cavity decreases caudad, the pelvis being a "bottle neck" to the outlet of the digestive, urinary, and genital system. The representatives of these three systems have some freedom of movement within the greater, but in the lesser pelvic cavity, they are all closely adherent to each other, so that within it there appears to be but one "visceral unit" (text figs. 33 and 35). In a general way, the peritoneal adhesions within the pelvic cavity of male are similar to those in female: differences do exist, these being related to differences in the structure of male and female urino-genital systems. In female, the insertion of the uteri and cephalic part of the vaginae between bladder and rectum, results in the development of an additional pair of peritoneal folds.

iii. Pelvic peritoneal folds in male (text figs. 32 and 33).—Rectum and distal part of left colon lie in the dorsal portion of the lesser and greater pelvic cavities respectively. Ventral to distal part of left colon and rectum is the urogenital system, the bladder being largely in the cavity of the greater and the urethra in that of the lesser pelvis (text fig. 33).

(a) Recto-vesical fold. As peritoneum, following the loss of a distinct mesocolon, loses its adhesion to lateral walls of first 10 mm. of rectum, so as to finally cover its ventral wall alone, it is reflected ventrad on the right, and left sides of rectum to dorso-lateral aspect of bladder. The effect of this reflection is to produce two vertical longitudinal bands, which support bladder. They are thought to be homologous with the right and left recto-vesical folds of human anatomy (Gray, 1916, p. 1073). The reflection from sides of rectum finally becomes transverse to its ventral wall, so that, at their caudal ends, a few millimetres cephalad to beginning of prostatic urethra, the right and left recto-vesical folds may be regarded as converging and becoming continuous (text fig. 32). These bands, when stretched and viewed from the side, are broadly speaking, of triangular shape, with apex of triangle pointing caudad. Thus the bands become narrower towards their caudal ends, this narrowing being associated with the close approximation of caudal end of bladder to rectum.

Each band may be considered to have three margins—two attached and one free.



Text fig. 32.—**S. brachyurus.** Ventral view of viscera of cephalic part of pelvic cavity in the male. Ventral portion of right and left pubis and ischium removed and bladder pulled caudad into lesser pelvic cavity covering the urethra. About natural size.

At A—mesocolon becoming detached from dorsal and lateral walls of the rectum; B—distended bladder; CAUD.—caudal end of pelvic cavity; CEPH.—cephalic end of pelvic cavity; FR.CAUD.—free caudal margin of right "inguinal fold" (which arises from right recto-vesical fold) with vas deferens running through it; FR.CEPH.—free cephalic margin of right recto-vesical fold; ISCH.—ischium (cut); L.DP.ING.RG.—left deep inguinal ring (internal abdominal ring); L.PARARECT.FOS.—left pararectal fossa; MUSC.—muscles (cut); PERIT.—peritoneum lining greater (false) pelvic cavity; PUB.—pubis (cut); R.RECT.-VES.F.—right recto-vesical fold; RECT.-VES.PCH.—recto-vesical pouch; TRANSV.—reflection of peritoneum covering ventral wall of rectum in a vertical transverse plane; UR.—ureter. Other abbreviations—see text figs. 18a and 20.

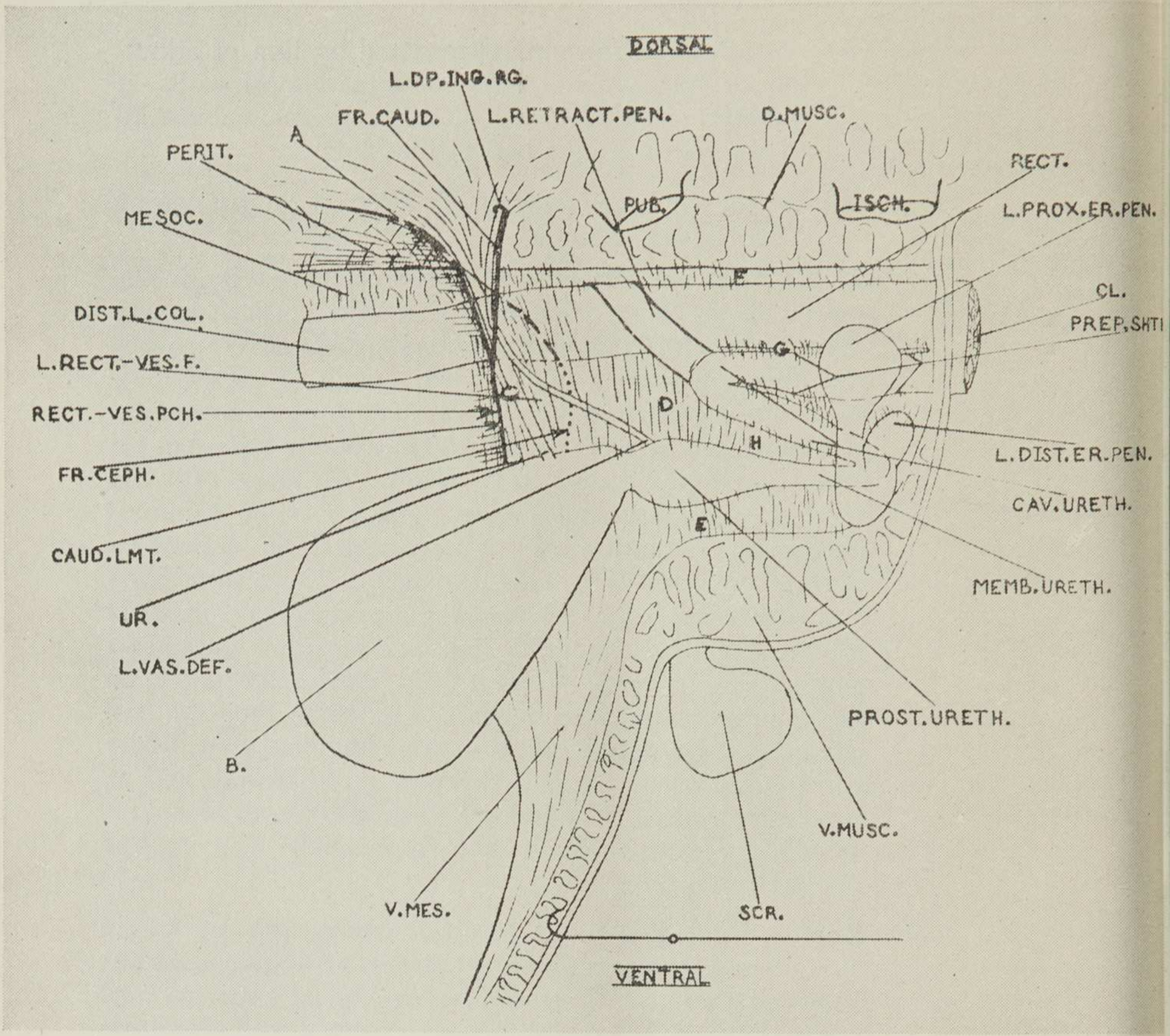
(i) An attached margin represented by line of reflection of peritoneum from lateral and ventral walls of rectum.

(ii) An attached margin represented by line of adhesion of recto-vesical fold to dorso-lateral walls of bladder. Cephalic end of this margin is about 40 m.m. from cephalic end of bladder.

(iii) A free cephalic margin, 20-25 mm. long, forming third side of triangle.

On the right and left sides of greater pelvic cavity, in the region of the brim of pelvis, is a fold of peritoneum, continuous with peritoneum lining greater pelvic cavity, and also with dorsal half of free magin of corresponding recto-vesical fold. Plane of each fold is horizontal and therefore at right angles to that of the recto-vesical fold (text figs. 32 and 33). Each, extending into the corresponding inguinal region, appears to be a lateral (inguinal) extension of recto-vesical fold, having a slightly concave free caudal margin, 20-30 mm. long and stretching from free cephalic margin of recto-vesical fold to the deep inguinal ring (or internal abdominal ring). Vas deferens of each side, after emerging from the inguinal canal into pelvic cavity, runs along the free caudal margin of the corresponding inguinal fold before turning to travel caudad through recto-vesical fold to prostatic urethra. Ureter in the last 30 mm. of its course to bladder, runs through recto-vesical fold near its free cephalic margin.

(b) Recto-vesical pouch. A cavity, which appears to be homologous with recto-vesical pouch of human anatomy (Cunningham, 1937, p. 621; recto-vesical excavation of Gray, 1916, p. 1072), lies between ventral wall of rectum and dorsal wall of bladder, and is bounded laterally by the recto-vesical folds (text fig. 32). It has been indicated that with the narrowing of the recto-vesical fold caudad, the bladder, towards its caudal end, is more closely applied to ventral wall of rectum. The effect of this, coupled with the final reflection in a vertical transverse plane of the peritoneum covering ventral wall of rectum (see p. 129), and the extensive connective tissue adhesions between distal parts of rectum and urogenital system (see later p. 138) is to reduce and finally close the cavity of the recto-vesical pouch caudad (text fig. 32). Recto-vesical pouch opens at its cephalic end into abdominal cavity by a mouth bounded by ventral wall of rectum, dorsal wall of bladder, and laterally by free cephalic margin of recto-vesical fold(text fig. 32). This mouth has a transverse width of 20-25 mm. and a dorso-ventral depth of 20-30 mm. Recto-vesical pouch has a cephalo-caudal length of about 10 mm., its caudal (blind) end being about 5 mm. anterior to cephalic end of prostatic



Text fig. 33.—**S. brachyurus.** Left lateral view of pelvic viscera of the male. Ventral portion of left pubis and ischium removed. Portion of ventral body wall has been pulled caudad and is shown in a vertical plane. 2/3 natural size.

CAUD. LMT.—caudal blind end of recto-vesical pouch; CAV. URETH.—cavernous uretha; D—connective tissue between cavernous uretha and ventral wall of rectum; DIST.ER. PEN.—distal erector penis; DIST.L.COL.—caudal end of distal left colon; D. MUSC.—cut muscles of dorsal pelvic wall; E—connective tissue between urethra and ventral wall of pelvis; F—connective tissue between rectum and dorsal wall of pelvis; FR.CAUD.—free caudal margin of left "inguinal fold" with vas deferens running along it; FR.CEPH.—free cephalic margin of left recto-vesical fold; G.—connective tissue between distal cavernous uretha plus preputial sheath, and ventral wall of rectum; H—conective tissue between membranous and proximal part of cavernous uretha; L.DP.ING.RG.—left deep inguinal ring (internal abdominal ring); L.ISCH.—left ischium (cut); L. PROX. ER. PEN.—left proximal erector penis; L. PUB.—left pubis (cut); L.RETRACT. PEN—left retractor penis; L.UR.—left ureter; MEMB. URETH.—membranous urethra; MESOC.—narrowing mesocolon; PREP.SHTH.—preputial sheath; PROST.URETH.—prostatic urethra; V.MES.—"ventral mesentery"; V.MUSC.—cut muscles of ventral pelvic wall. Other abbreviation—see text figs. 10, 12, 20 and 32.

urethra, and 50-60 mm. from cephalic end of cloaca (text fig. 33).

(c) Pararectal fossa (text fig. 32). Recto-vesical pouch extends dorsad on either side of beginning of rectum or end of left colon, to form what appears to be the rather ill defined homologue of the pararectal fossa of human anatomy (Gray, 1916, p. 1073); Cunningham, 1937, p. 621).

iv. Pelvic peritoneal folds in the female (text figs. 34 and 35). As in male, rectum and distal part of left colon lie in dorsal portion of lesser and greater pelvic cavities respectively. Uteri, the caudal half to two-thirds of which are in contact along middle line (text fig. 34), and cephalic end of lateral vaginae and median vagina, lie ventral to distal end of left colon and proximal end of rectum. Ventral to uteri is bladder; urethra is ventral to median vagina. Urino-genital sinus is in caudal part of lesser pelvic cavity and ventral to caudal part of rectum (text fig. 35).

By the same process and through about the same space as described for male, the mesocolon, in the region of brim of pelvis, just dorsal to cephalic end of contact between right uterus and left, loses its identity (text fig. 35). Peritoneum no longer adheres to dorsal and lateral walls of cephalic part of rectum, but merely covers a portion of its ventral wall.

(a) Recto-uterine fold (text fig. 34). In losing adhesion to rectum, the peritoneum is reflected from right and left edges of its ventral wall to dorsal wall of caudal part of right and left uterus, and thus two vertical longitudinal bands of peritoneum are produced which appear to be homologous with the right and left recto-uterine folds of human anatomy (Gray, 1916, p. 1169; Cunningham, 1937, p. 740).

Caudad, as in male, the reflection becomes transverse to ventral wall of rectum, so that, at their caudal ends, the right and left bands may be regarded as converging and becoming continuous.

Each recto-uterine fold is continuous with the broad ligament, which arises as a reflection of peritoneum lining dorsal wall of greater pelvic cavity, rather than as a fold of peritoneum covering ventro-lateral walls of rectum (cf. recto-uterine folds) (text figs. 34 and 35). Mackenzie (1919, p. 25), in describing the general plan of the broad ligament in marsupials, states that it suspends ". . . the ovary, fimbriated apron, oviduct and uterus, together with the commencement of the urino-genital canal." In *Setonix* the broad ligament, beyond its attachment to ovary, extends a considerable distance up into the abdominal cavity. This extension has a free cephalo-ventral margin.

In this paper recto-uterine folds are considered to extend along uteri as far as the cephalic end of contact between uteri. Here the broad ligaments, with which the recto-uterine folds are continuous, are considered to begin (text fig. 34).

Thus, in being continuous with the broad ligaments, recto-uterine folds, unlike recto-vesical folds of male and utero-vesical folds of female (described later), have no free cephalic margin. Each has two attached margins, represented by the line of reflection of peritoneum from rectum, and by the line of its adhesion to right and left uterus.

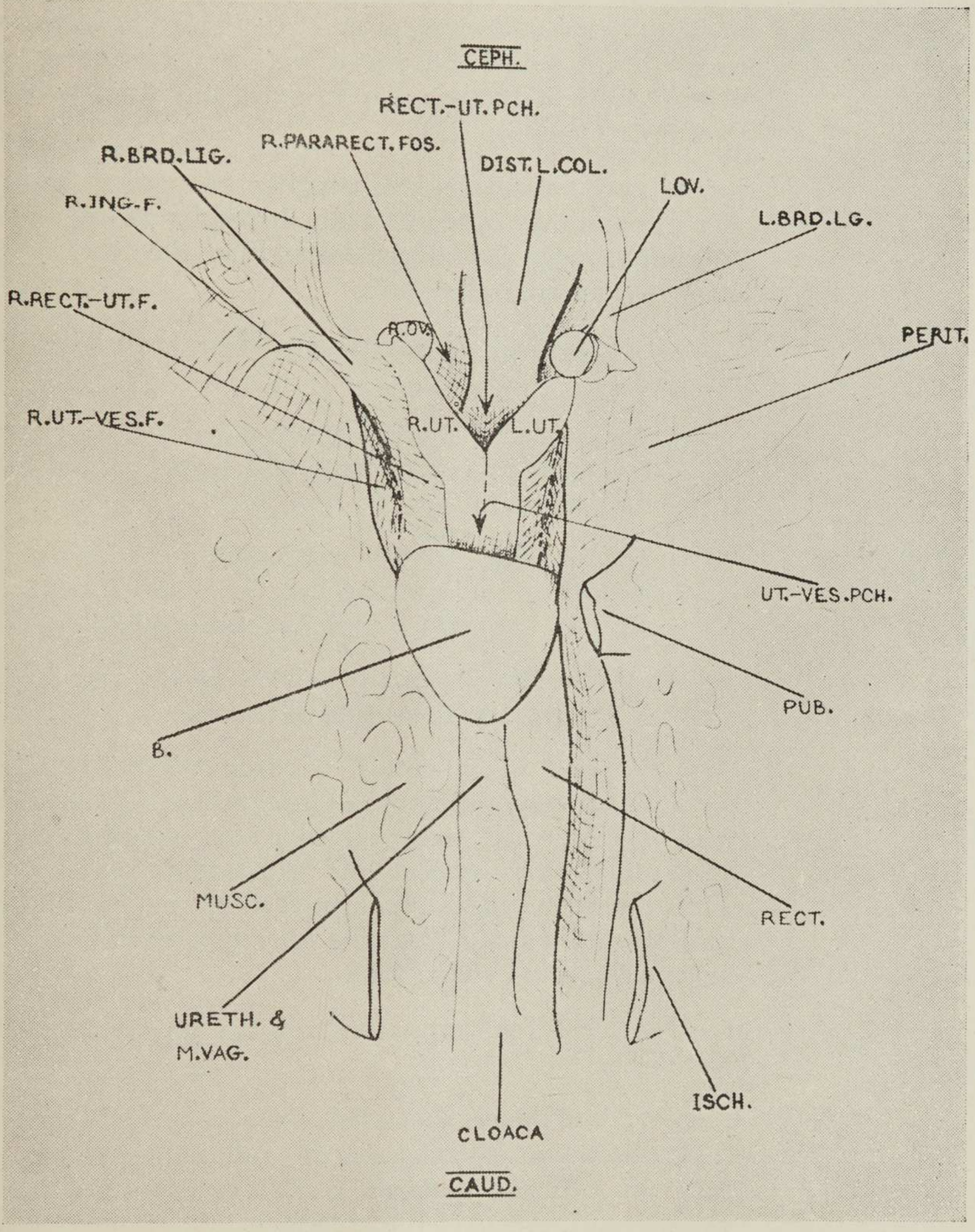
Recto-uterine folds appear to serve as supports for caudal end of ends of uteri. This is an addition to that provided by the broad ligament.

(b) Recto-uterine pouch. A cavity lies between ventral wall of rectum and dorsal walls of caudal ends of uteri, and is bounded laterally by the recto-uterine folds. This appears to be the homologue of the recto-uterine pouch of human anatomy (Gray, 1916, p. 1072; Cunningham, 1937, p. 621).

As the genital system approaches the more confined space of lesser pelvic cavity from greater pelvic cavity, it becomes less mobile and lies closer to rectum. The effect of this, combined with the final reflection, in a vertical transverse plane, of peritoneum covering ventral wall of rectum (see p. 133) and the extensive connective tissue adhesions between distal parts of rectum and genital system, is to reduce and close the cavity of the recto-uterine pouch caudad. Pouch opens into abdominal cavity by a mouth at cephalic end of contact between uteri, bounded by ventral wall of rectum, dorsal wall of bladder, and, laterally, by the continuous structures formed from recto-uterine folds and broad ligaments (text fig. 34). Mouth has a transverse width of about 10 mm. and a dorso-ventral depth of about 15 mm. Pouch has a cephalo-caudal length of 13-20 mm. Its blind end is about 40 mm. from cephalic end of cloaca.

(c) Pararectal fossa (text fig. 34). Female, like male, has a right and left pararectal fossa devoloped on either side of rectum, as dorsal extensions of recto-uterine pouch. In the specimens examined, the fossae were not well marked. They lie on either side of distal part of left colon and beginning of rectum, and become less distinct as the peritoneum, supporting distal part of hind-gut, moves from its dorsal to its ventral side. Each fossa is bounded laterally by the broad ligament of uterus.

(d) Utero-vesical fold (text figs. 34 and 35). Arising on each side of pelvic cavity as a reflection of recto-uterine fold and caudal half of broad ligament, and extending to



Text Fig. 34.—**S. brachyurus.** Ventral view of viscera of greater and lesser pelvic cavities of the female. Ventral portion of right and left pubis and ischium removed. The cephalic end of bladder (empty) has been pulled caudad into lesser pelvic vacity. Natural size.

CAUD.caudal end of pelvic cavity; CEPH.—cephalic end of pelvic cavity; M.VAG.—medium vagina R. & L.BRD.LIG.—right and left broad ligaments; R.ING.F.—right inguinal fold of broad ligament (left not shown); R. PARARECT.FOS—right pararectal fossa R.RECT.-UT.F.—right recto-uterine fold; RECT.-UT.PCH.—into recto-uterine pouch; R.OV.—right ovary; R. & L.UT.—right and left uterus; R.UT-VES.F—right utero-vesical fold; URETH.—uretha; UT.-VES.PCH—into utero-vesical pouch. Other abbreviations see text figs. 18a, 20, 29 and 32.

dorsal wall of bladder, is another vertical fold of peritoneum, which, as it arises from the recto-uterine fold and not from the peritoneum investing uterus, is not strictly *utero-vesical*. The line of its reflection is roughly midway between the reflection of the broad ligament and recto-uterine fold from dorsal wall of pelvic cavity and ventral wall of rectum respectively, and their adhesion to uterus (text fig. 35).

Each utero-vesical fold is roughly triangular, apex of triangle pointing caudad. Thus the fold narrows towards its caudal end, and at the same time the bladder gets closer to the genital system.

Each utero-vesical fold may be considered to have three margins—

(i) An attached margin represented by the line of reflection of fold from broad ligament and recto-uterine fold.

(ii) An attached margin represented by line of adhesion of fold to bladder. The attachment ends 15 to 21 mm. from cephalic end of bladder.

(iii) A free cephalic margin, between 20 and 30 mm. long, forming third side of triangle.

Cephalic end of reflection of each utero-vesical fold from the corresponding broad ligament and recto-uterine fold, is about 10 mm. anterior to cephalic end of adhesion of utero-vesical fold to bladder (text fig. 35). Thus the free cephalic margin of utero-vesical fold runs ventrad and caudad from the reflection from broad ligament and recto-uterine fold.

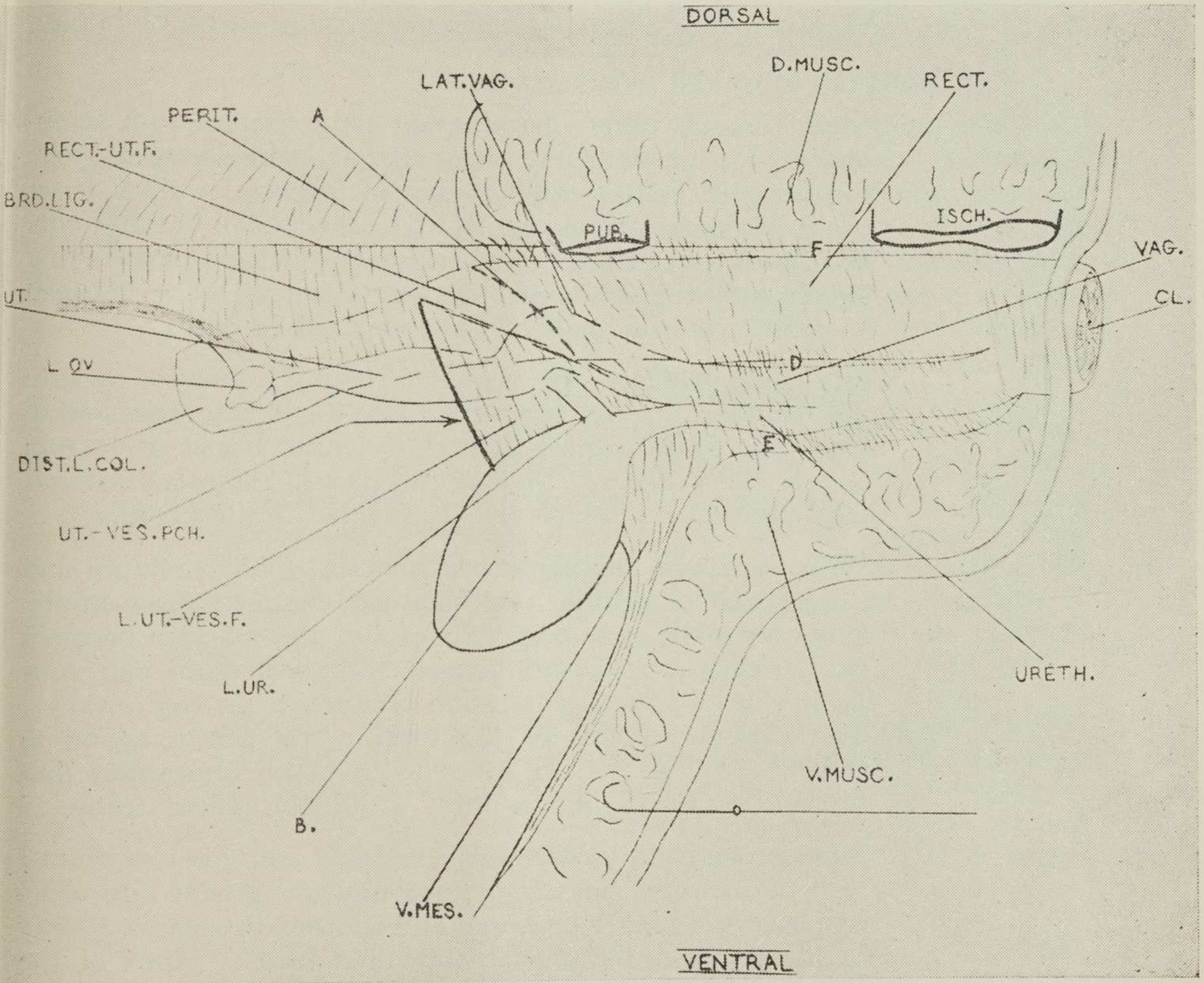
Utero-vesical folds apparently form dorsal support of bladder.

(e) Utero-vesical pouch (text figs. 34 and 35). There is a cavity between ventral walls of caudal ends of uteri and those of cephalic ends of lateral vaginae and median vagina, and dorsal wall of bladder. It is bounded laterally by utero-vesical folds and appears to be the homologue of utero-vesical pouch of human anatomy; (Cunningham, 1937, p. 701). Through the growth of connective tissue, caudal end of bladder and urethra are close to median vagina. Thus the cavity of utero-vesical pouch is reduced and finally closed caudad (text fig. 35). It opens at its cephalic end into abdominal cavity by a mouth bounded by ventral walls of uteri, dorsal wall of bladder, and laterally by the free cephalic margins of utero-vesical folds (text fig. 34). Mouth has a transverse width of between 8 and 19 mm. and a dorso-ventral depth of between 8 and 17 mm. Pouch has a cephalo-caudal length of between 13 and 18 mm., its blind end being 33 to 40 mm. from cephalic end of cloaca.

Terminal part of ureter in female runs through recto-uterine and utero-vesical folds to bladder (text fig. 35).

v. Preliminary note on ventral peritoneal fold ("ventral mesentery") in males and females (text figs. 33 and 35).

In both male and female there is a prominent vertical fold of peritoneum extending from ventral wall of bladder to ventral body wall, along which it extends some distance from the pelvic into the abdominal cavity. Together with recto-vesical folds in male and utero-vesical folds in female,



Text Fig. 35.—**S. brachyurus.** Left lateral view of pelvic viscera of female. Ventral portion of left pubis and ischium removed. Portion of ventral body wall has been pulled caudad and is shown in a vertical plane. Natural size.

At A—mescolon becoming detached from dorsal and lateral walls of rectum; D—connective tissue binding urogenital system to rectum; E—connective tissue binding urogenital unit to ventral pelvic wall; F—connective tissue binding rectum to dorsal pelvic wall; L.RECT.-UT.F.—left recto-uterine fold; L.UT.-VES.F.—left utero-vesical fold; LAT. VAG.—lateral vagina (broken line); VAG.—caudal end of vaginal sytsem (medium vagina and lateral vaginae closely bound together). Other abbreviations—see text figs. 10, 18a, 20, 29, 33 and 34.

it helps to retain the bladder in position. The folds may be imagined to have three margins—

(a) An attached margin, represented by the line of reflection of peritoneum from ventral wall of bladder. Its cephalic end 10 to 30 mm. from cephalic end of bladder.

(b) An attached margin, represented by line of reflection of peritoneum from ventral body wall.

(c) A free, concave, cephalic margin, which, owing to the cephalic end of (b) being well in advance of the cephalic end of (a), runs cephalo-ventrad from bladder to ventral body wall.

Ventral fold of peritoneum has a maximum width of 45 mm.

vi. Relations of caudal part of rectum.

(a) Male (text fig. 33). Termination of mesocolon with beginning of rectum does not imply that it lacks dorsal support, for along its entire length it is held to dorsal wall of lesser pelvic cavity by connective tissue. The caudal 50 to 60 mm. of rectum, i.e., of the rectum caudal to end of recto-vesical pouch, has, in addition, connective tissue extending between it and the *lateral* walls of the lesser pelvic cavity.

Stretching between the cephalic 10 to 15 mm. of rectum and bladder, are the recto-vesical folds. These arise rather from the ventro-lateral than the ventral aspect of rectum (see p. 129). Ventral wall of this part of rectum is covered with peritoneum, which is not reflected to the bladder.

With the narrowing of the recto-vesical fold as rectum and caudal part of bladder approach the confined space of the lesser from the greater pelvic cavity, the bladder becomes more closely applied to ventral wall of rectum and connective tissue adhesions develop between them (see p. 131). The various sections of the urethra are firmly bound to ventral wall of rectum so as to give the impression that there is but one "visceral unit" within the pelvic cavity.

The prostatic and cavernous urethrae are close to ventral wall of rectum. The cavernous urethra is bent into a V-shape with a longer proximal and shorter distal arm, tightly bound together by tough connective tissue. Apex of the V points cephalad. Proximal arm of cavernous urthera has connective tissue extending ventrad from it to the membranous urethra (text fig. 33). Distal arm is closely bound to ventral wall of rectum. Preputial sheath, enclosing the glans penis, is bound by connective tissue to ventral wall of rectum. (For details of male genital system in Marsupials see Mackenzie 1919, pp. 81-100).

Urethra is also bound to ventral wall of lesser pelvic cavity by connective tissue.

Retractores penis leave cavernous urethra at the apex of its V and extend cephalo-dorsad over each side of middle part of the rectum, to which they are closely bound by connective tissue.

On right and left sides of caudal end of rectum, just before the beginning of cloaca, is a proximal erector penis. Distal erectores penis, being smaller and not extending so far dorsad as the proximals, are not so closely related to rectum.

(b) Adhesions in female (text fig. 35). Rectum in female, as in male, is bound along its entire length to dorsal wall of lesser pelvic cavity by strands of connective tissue. Caudal 40 mm. of rectum, i.e. rectum caudal to blind end of recto-uterine and utero-vesical pouches, has connective tissue extending between it and the lateral walls of pelvic cavity.

Stretching between cephalic 10 to 20 mm. of rectum and uteri, are the recto-uterine folds, and, associated with them are the utero-vesical folds. Recto-uterine folds arise as reflections of peritoneum covering ventro-lateral walls of rectum (see p. 133). Ventral wall of this cephalic part of rectum is covered with peritoneum, which is not reflected to bladder. With the narrowing of recto-uterine folds, as rectum and caudal parts of uteri approach the confined space of the lesser from the greater pelvic cavity, the uteri become more closely bound to rectum and connective tissue adhesions develop between them (see p. 134). Utero-vesical folds also narrow caudad, so that caudal part of bladder becomes closer to the median vagina(see p. 136). Urethra is bound to median vagina by connective tissues (see p. 136). Through the last 40 mm. rectum is closely bound, first to vaginal system and then, farther caudad, to urogenital sinus.

Genital and urinary systems, before their junction to form the urogenital sinus, are closely bound together. Urethra and median vagina form a unit, which, with the urogenital sinus, is bound by connective tissue, not only to ventral wall of rectum, but to lateral and ventral walls of lesser pelvic cavity.

d. Conclusion on rectum and preliminary note on uro-genital genital system of an adult female *Setonix.*

From the preceding description it can be seen that, within the cavity of the lesser pelvis in both male and female, digestive and urogenital systems are closely applied to each other, forming a compact mass and giving the appearance of being but one "visceral unit."

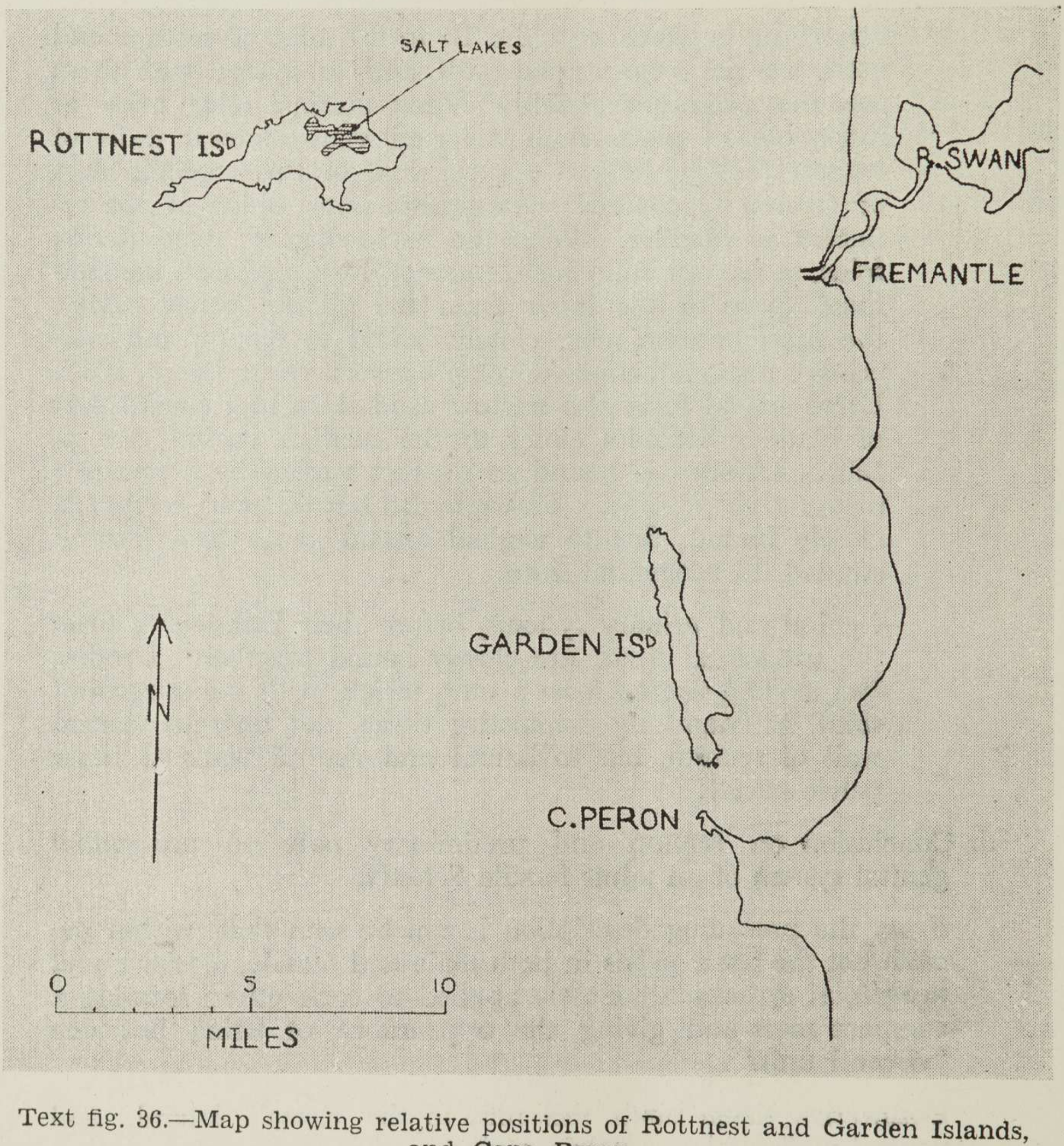
Connective tissue binds this unit to the dorsal, lateral, and ventral walls of lesser pelvic cavity, so that rectum and urethra in male, and rectum, vaginae, urethra, and urogenital sinus in female, are extremely immobile. This contrasts with the contents of the greater pelvis cavity, which by comparison, have much more freedom of movement, but whose mobility decreases as they approach the cavity of the lesser pelvis. Brief examination of the genital system of one adult female showed that—

i. Lateral vaginae were 35 mm. long.

ii. Urogenital sinus, formed at point of coalescence of lateral vaginae (i.e. no post vaginal sinus) was 18 mm. long.

iii. Urethra was 15 mm. long.

iv. Caudal end of bladder is attached about halfway along the median vagina.



Text fig. 36.—Map showing relative positions of Rottnest and Garden Islands, and Cape Peron.

IV. NOTES ON NATURAL HISTORY OF THE QUOKKA.

A. THE SEPARATE OCCURRENCE OF *Macropus eugenni* ON GARDEN ISLAND AND OF *Setonix brachyurus* ON ROTTNEST ISLAND.

(Text fig. 36.) (N.B.: Glauert, 1920, p. 45 "Summary.")

Both species are recorded from the mainland of Western Australia (Shortridge, 1909, pp. 812-813; Glauert, 1934, p. 32). At present they are rare on the Swan Coastal Plain.

M. eugenni occurs in large numbers on Garden Island, south of Fremantle, and *S. brachyurus,* though not recorded from Garden Island, is equally abundant on Rottnest Island, west of Fremantle. Early French naturalists described an animal 65 cm. high from Rottnest in addition to a rat-like form: the former has been regarded as *M. eugenii,* the latter as *S. brachyurus.* Shortridge (1909, p. 813) recorded *M. eugenii* from Rottnest, but it has been suggested to me that his and the French naturalists's identifications were incorrect and that *M. eugenii* has never existed on Rottnest; it certainly does not seem to be extant on Rottnest now. Glauert (1934, p. 32) does not record *M. eugenii* or *M. derbianus* (probably really a sub species of *eugenii*), from Rottnest. If it was once present on that island, why should it have perished and *Setonix* have survived?

Rottnest and Garden Islands are both fairly well isolated from the mainland—Rottnest, the long axis of which runs east and west, being 11½ miles, and Garden Island, which trends north and south, being only a little more than a mile offshore at its nearest point (text fig. 26). The environment on the islands is similar, both being characterized by absence of indigenous eucalypts, and presence of dense thickets of *Acacia.* Apart from size, Rottnest differs from Garden Island in having several salt lakes and also small areas of grassy heath. On Rottnest there was formerly a freshwater swamp, which is reported to have been drained within the last few years; also, in some places, fresh water, soaking down through the sand and limestone of which the island is composed, oozes out to form very small "soaks." It is reasonable to expect similar sources of water on Garden Island. *M. eugenii* and *S. brachyurus* might therefore be expected to live on either island.

Why is it then, that these islands, not far from the mainland nor from each other, and, according to geologists, only separated from the mainland in Recent or sub-Recent times (Clarke, Prider and Teichert, 1944, p. 285), should each, apparently, have its own particular macropod, although both forms exist on the mainland?

It is suggested that at the time when Garden Island and Rottnest formed part of the mainland, the physically inferior forms, such as *M. eugenii* and *S. brachyurus,* were driven by larger macropods from the richer land round the Swan River estuary to the poorer coastal sandhills. If so, the two forms would co-exist on the north-directed promontory formed of the cojoined Cape Peron, Garden and Rottnest Islands, *Setonix,* being physically inferior to *M. eugenii,* would migrate towards the end of the promontory (the present Rottnest), leaving *M. eugenii* in the Garden Island-Cape Peron region. Subsequently the promontory was separated from the mainland and divided in two, Rottnest, inhabited by *Setonix,* being the remains of its northern tip, and Garden Island, inhabited by *M. eugenii* being its base.

B. METHOD OF CAPTURE AND OBSERVATIONS ON THE QUOKKA IN CAPTIVITY.

Seven specimens of *S. brachyurus* were kept alive in a large, earth-floored, open air cage at the Department of Biology in the University of Western Australia. With the exception of one specimen, which was "run down" in a fence corner, they were caught at night by Mr. N. Love, of the Rottnest Board of Control. I do not know exactly how he caught them possibly in the same way as a party of students caught a specimen of *M. eugenii* in November, 1946. Like the quokkas the "Garden Island wallabies" are fairly tame and, at night, move into the deserted settlement at Garden Island, probably from past habit, looking for scraps around the huts. By diverting the selected animal's attention with food, four persons, each carrying an electric torch, which was directed at the wallaby's eyes, surrounded and slowly approached it to within a few yards. The animal now got frightened and began to move slowly out of the circle of people, but after a short chase, with the wallaby in a confused state, it was captured. I am told that if one person directs a very powerful torch at the eyes of a quokka, a second person can approach from behind and catch the animal by the tail.

In captivity the quokka can live on a varied diet—household scraps, blue lupins (*Lupinus angustifolius*), thistle, grass and the leaves and flowers of a native wattle (*Acacia cyanophylla*) which grows round the University, were all acceptable. (Incidentally, the principal Rottnest acacias are *A. cuneata, A. cyclopsis,* and *A. rostellifera*).

Though usually crepuscular or nocturnal in the wild state, in captivity the animals were quite active during the day.

When feeding the quokka makes considerable use of the forelimb, which is surprisingly mobile, picking up or removing foreign matter from food with the hand and holding food to the mouth while it is eaten. Finlayson (1930, p. 51) notes a well developed power of grasp in *Macropus* (*Wallabia*) *ruficolis typicus.* Several times the caged quokkas were seen squatting on their hindquarters, with the tail tucked up between the hind limbs, its dorsal (superior) surface lying on the ground. Sometimes, with the tail in this position, the head is tucked down between the legs so that the animal is almost rolled up into a ball (see also Fleay, 1936, p. 153). When alarmed the quokka may emit a hissing sound and thump the ground with its foot (a common habit with the macropods).

C. "BIRTH HABITS" AND SUBSEQUENT EVENTS.

On 7/6/46 at 4.00 p.m. a quokka was noticed sitting in the corner of its box with its tail between its legs (the position described above), and clawing with its hands the fur near the cloacal opening. Occasionally it stopped clawing and licked the fur in the pubic region, thus forming a distinct track through the fur from the opening of the cloaca to the mouth of the pouch. While these actions were going on, there was a violent quivering of the abdomen and hindlimbs.

At 4.20 p.m. the animal, being disturbed, ceased these toilet activities, and leaving the box, began to feed. Five minutes later it had returned to its original position in the box and began further licking of the fur. During the preceding disturbance the definition of the track from cloaca to pouch was lost. The animal had now become much more nervous, concentrating less on the licking process. Clawing action was again seen, followed by a holding open of the mouth of the pouch with the hands. The mouth and inside of the pouch then apparently received toilet attention, the muzzle being thrust into the pouch. This was followed by a general toilet of the head and forearms. The forearm having been thoroughly licked and moistened, was used to rub the face.

At 4.50 p.m. the animal, after completing the toilet of the head, neck, shoulders, and thorax, came out of the box and began feeding with the other animals.

During the period in which these activities were observed, there was no sign of birth. The ground in the box was subsequently searched unsuccessfully for a pouch embryo, as, if born, it might have been dislodged from the parent. The activities were very similar to those described as "birth habits" by Fleay (1936, pp. 153-5) for the quokka in captivity. Subsequent events were interesting.

By 26/6/46 there was one surviving female; the other, present on 7/6/46, had died and its pouch was empty. At 11.30 a.m. on 26/6/46 the surviving female, believed to be the one whose toilet (birth) activities have been described, was observed with its tail between its legs, licking and clawing the region of the mouth of the pouch. It then hopped into its box and began eating something that it held in its hands. Investigation showed that the object was a well advanced pouch specimen which was still warm. The mother had begun eating the pouch embryo, the entire tail, the left hindlimb, portions of the pubic region, and the right hand being mission. Sex could not be determined owing to this damage.

Total length of this embryo, from tip of rhinarium to region of base of tail, was about 110 mm. Head 30 mm. long. Tongue was visible. Mouth, losing its circular outline, was becoming more slit-like, as in the adult. Lower pair of incisors visible. There was slight pigmentation of tip of muzzle. Rhinarium well formed, the median cleft and crescentic nostrils being obvious. Papillae of the mystical vibrissae prominent and hair was visible round upper lip. Eyelashes could be seen on the upper eyelid, and the eyes, though closed, were well formed. Ears, about 5 mm. long, and dark grey. Head and body, apart from limited areas of grey pigmentation at tip of muzzle and on distal parts of hand and foot, pale pink. Only hairs visible were the mystical vibrissae, hairs around upper lip, eyelashes, and very short hairs on back of hand. Fingers and toes had the brown claws well developed. Palm of hand granular. Syndactyly, obvious. Bones of head, well ossified. Ribs, scapula, skeletal structures of fore and hind limb, and pelvis could be felt and were prominent. Thus the pouch embryo was fairly well advanced in its development. It had either died in the pouch (why then was it still warm?) and been deliberately removed by the parent, or, because of the loose attachment to the nipple, as indicated by the mouth having become more slit-like, had been accidentally thrown out during the mothers' activities and thus killed.

If the adult specimen involved in these later observations was that whose toilet was watched on 7/6/46, then the following explanations are possible:—

(1) If, on 7/6/46 when the adult female was performing its toilet as described, a young animal (the well advanced embryo described) was born, then there is evidence of very rapid development after entry into the pouch, for it must have grown from a rather shapeless animal no more than 10 mm. (½in.) long (see Fleay, 1936, p. 153) to the large pouch embryo.

Fleay (1936, pp. 154-5) shows indeed that the pouch embryo of the quokka does develop very rapidly, but, in the case he describes, the head and body had grown to 2½in. (about 65 mm.) in two months and was dark bluish pink in colour. In the case described here, if birth occurred on 7/6/46, the head and body of the embryo had developed to 110 mm. in 19 days and was still not markedly pigmented. Such rapid growth seems unlikely.

(2) Fleay (1936, p. 153) says of *Setonix* that only one embryo is carried in the pouch. Abbie (1941, p. 86) mentions, as occurring in marsupials in general, super-foetation and the survival of spermatozoa in the female tracts for long periods. Is it possible that on 7/6/46, despite Fleay's statement (1936, p. 153), a second embryo was born, the pouch already containing one specimen which subsequently grew to the 110 mm. form described above? After 26/6/46 the pouch was empty. If, then, an animal was born on 7/6/46, it presumably fell to the ground and was lost in the sand despite my searchings.

(3) Although no record was made of it, I may have had a rather violet chase before I caught and handled the suspected mother, twelve or more hours before it began the toilet activities. It is suggested that the animal, although it already had an embryo in the pouch, was disturbed in such a way by this excessive activity as to induce an imitation of the birth habits.

D. WORMS PARASITIC ON THE QUOKKA.

Several nematode worms were removed from dissected quokkas. They were up to 15 mm. long, 1 mm. thick, and of a pale colour. They were found in the regions of the greater omentum, mesial fold, and pelvic cavity. Small cyst-like structures, up to 10 mm. across, were also found in the greater omentum. They were hard and, when broken, appeared to be made up of a number of small tubes or cavities.

V. CONCLUSION ON WHOLE PAPER.

No inferences as to the phylogenetic position of *S. brachyurus* in the family Macropodidae have been drawn from this study of its externals and hindgut. Gregory (1910, pp. 11-12) and Pearson (1946, pp. 21 and 25) have pointed out that conclusions as to the phylogenetic position of an animal, based on the study of structures closely related to environment (teeth, claws or hoofs, digestive system), are not as reliable as conclusions based on the study of organs not so easily affected by external conditions (brain, reproductive organs, foramina of the skull, auditory ossicles). Beddard (1908) and Mitchell (1916) have, however, drawn some conclusions regarding classification from studies of the gut pattern of animals.

Bensley (1903, pp. 151-2; p. 202) after a study of the teeth and feet of macropods (among other marsupials), assigned a certain position to *Setonix* in the family. To verify or amend his conclusions all anatomical systems should be considered. In this paper there is a short note on the urogenital system of one female (p. 139). Further work in this field, with references to Pearson's (1944, 1945, and 1946) work on the urogenital system of marsupials, should be valuable in determining the relationship of *Setonix* to other macropods.

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PLATE I.—The quokka in captivity. N.B.: The white spot over the animal's (left) eye is not a "marking" of the fur, but a bare patch resulting from injury.

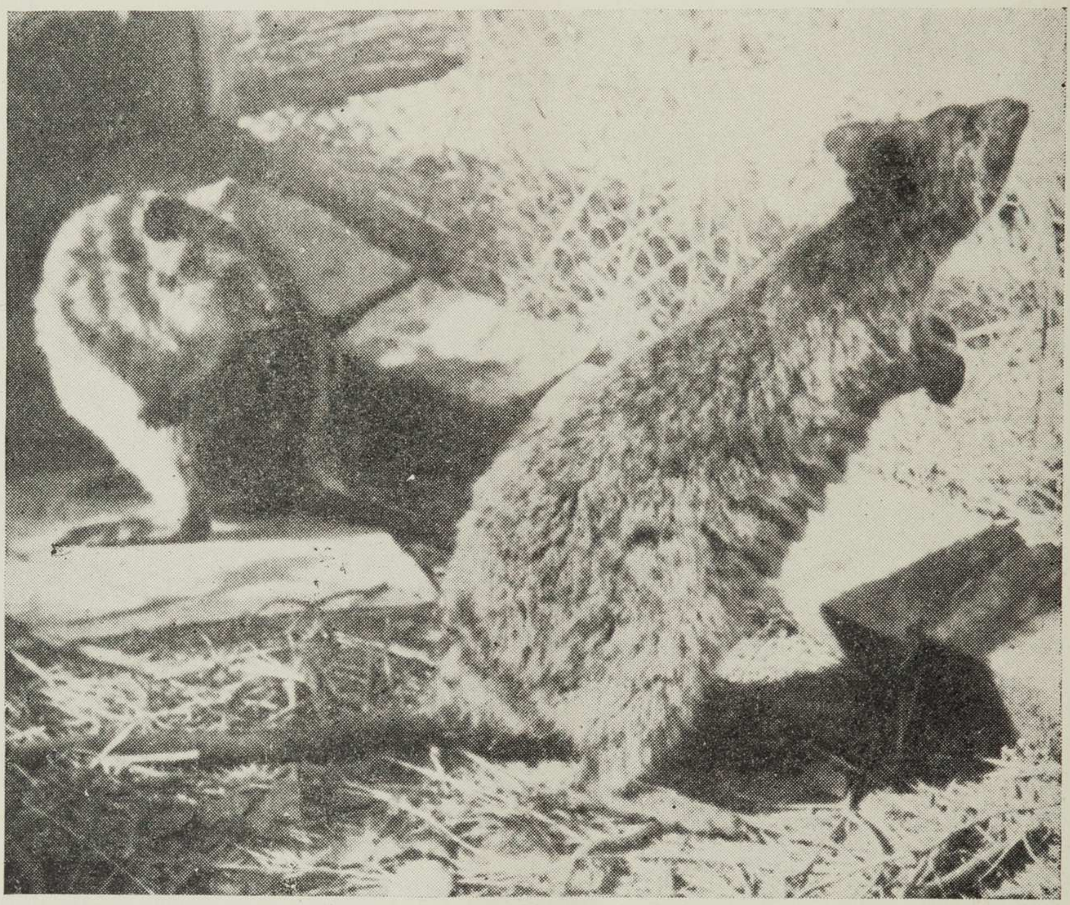

PLATE II.—Two captive specimens of the quokka (**S. brachyurus**). The animal on the right of the photo. is stretching for food held above it.